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Restoration ecology of ecosystems invaded by *Triadica sebifera* (Chinese tallow tree): theory and practice

by

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ABSTRACT

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Invasive exotic species threaten biodiversity and ecosystem functions globally, creating need for and encumbering ecological restoration. When restoring exotic plant-dominated ecosystems, reinvasion pressure is the rate of new exotic recruitment following mature exotic removal. It can vary broadly among similarly invaded habitats and is crucial to restoration outcomes and costs, but is difficult to predict and poorly understood.

Initial results from the experimental restoration of a wetland dominated by *Triadica sebifera* led us to develop the 'outgrow the stress' hypothesis. It holds: (1) Variation in reinvasion pressure is driven by differences in propagule abundance and spatiotemporal availability of realized recruitment windows, which are defined by abiotic conditions and biotic interactions. (2) Differences in reinvasion pressure become masked by exotic dominance when increases in niche breadth during development enable exotic persistence across sites where recruitment windows range from frequent to episodic.

We validated this hypothesis. First, we used greenhouse and field experiments to quantify *Triadica*'s moisture niche early in development. By two months post-germination, seedling tolerances broadened to include conditions unsuitable for

germination. This clearly demonstrated a rapid ontogenetic niche expansion, which could decouple mature *Triadica* density and average reinvasion pressure.

Second, we used a greenhouse mesocosm experiment to quantify how recruitment window duration, competition and fertility impacted population-level *Triadica* establishment in stressful environments. As 'outgrow the stress' predicts, longer windows increased *Triadica* success and multi-factor interactions were common, with competition and fertility effects varying among environmental contexts.

Third, we substantiated predictions of 'outgrow the stress' regarding propagule availability and soil moisture by manipulating these in a multi-site field experiment spanning eleven experimental restorations of *Triadica*-dominated habitats along a moisture gradient. *Triadica* reinvasion pressure varied broadly among sites but correlated with moisture and fertility. Propagule availability drove reinvasion in favorable environments, but availability of suitable conditions trumped propagules in extreme environments. Competition reduced *Triadica* performance and sometimes survival. *Triadica* prevalence reduced native plant prevalence. Six restorations require minimal *Triadica* management for success.

This work advances our understanding and enables better predictions of reinvasion pressure and invasions in general. Accurate predictions enhance restoration efficiency by informing site selection and optimal management strategies.

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CHAPTER ONE

Introduction and Summary

OVERVIEW

A fundamental goal of ecology is to understand the processes governing assembly, stability and change in ecological communities. Ecological succession, or the ordered progression of communities through distinct seres defined by characteristic species or functional groups, has remained a central topic in ecology since the nascence of the discipline. Essential to community level phenomena such as succession are processes of invasion (*sensu lato*), maintenance and extinction among individual species. Vital to these population level phenomena are processes of dispersal, establishment and reproduction among individuals themselves, which ultimately depend upon phenotypic expressions of genetic traits that govern individual physiological and behavioral characteristics in stochastic environments.

One of the most direct applications of our knowledge of ecological succession is the act of ecological restoration, which attempts to assemble communities with particular ecological features and/or functions by actively managing land in particular ways to "guide" succession along particular paths or to accelerate the development of particular conditions. One of the most direct applications of our knowledge of invasion is in the act of exotic species management, which attempts to extirpate, control or contain non-indigenous species with significant negative ecological and/or economic impacts on recipient ecosystems (i.e. "invasive species"). Given the current rate of decline in biodiversity resulting from habitat loss, invasive species and their interactions, research investigating ecological concepts important to the theory and practice of ecological restoration and invasive species management is of considerable importance to the preservation of biological diversity.

Overall, my dissertation research emphasizes community level processes most pertinent to restoration and invasive species ecology. My work specifically focuses on increasing our understanding of the factors and mechanisms underlying reinvasion pressure, particularly in restored wetlands and grasslands. To this end, I have utilized traditional field, mesocosm and greenhouse experiments, as well as experimental restorations of ecosystems invaded by Chinese tallow trees (*Triadica sebifera*) in southeastern Texas as a model system. Just as succession depends on populations and populations depend on individuals, my broad questions about communities (Chapter Two) first prompted specific questions about individuals (Chapter Three) and then populations (Chapter Four) that naturally generated specific questions about communities (Chapter Five) which meaningfully address and elucidate the mechanisms governing reinvasions pressure and the outcomes of ecological restoration and exotic management.

A fundamental goal of my dissertation has been to integrate restoration, invasion and community ecology and to test basic ecological theory while simultaneously devising more successful and efficient management strategies. By using the approaches above, I have been able to identify previously unreported and unrecognized processes influencing reinvasion pressure in general and to quantify their effects during restorations of ecosystems invaded by Chinese tallow trees.

CHAPTER TWO – Development of the 'outgrow the stress' hypothesis

Chapter Two is a conceptual paper resulting from insight gleaned from a great deal of empirical research performed over the course of my graduate studies not fully represented by this thesis. The full details of this additional work will become public in

the near future, but this conceptual paper, published in the September 2012 issue of *Restoration Ecology*, is a good synthesis of key theoretical findings.

Here I identify, formally describe, and review literature concerning three key concepts that are foundational to this thesis. First is reinvasion pressure, a factor of great concern to restoration practitioners but poorly understood and understudied. I argue that reinvasion pressure is crucial to restoration costs and outcomes, and review evidence that it varies widely among different species and systems. I discuss the benefits to restoration efficacy and efficiency that accurate estimates of average reinvasion pressure can provide, particularly as decision making tools for site selection and development of optimal management strategies. I identify key gaps in our knowledge that impede accurate estimates and identify a key ecological factor vital to obfuscating differences in reinvasion pressure.

That factor is the second key concept: ontogenetic niche expansions, which are increases in niche breadth during development. Niche expansions enable plants to persist in conditions unsuitable for their recruitment. In habitats that vary temporally, especially between years due to interannual variation, exotics with niche expansions can come to dominate over time even if their long-term average recruitment success is very low. Where this happens, exotic density and average reinvasion pressure become decoupled, and underlying differences producing low reinvasion pressure are masked. A key consequence of this phenomenon is the existence of exotic-dominated habitats that may be restored relatively inexpensively and with relatively high likelihoods of success, but which are difficult to detect (i.e. “cryptic opportunities”).

I then propose the 'outgrow the stress' hypothesis. The formulation and validation of this novel invasion hypothesis could be considered the singular contribution of my dissertation to modern ecological theory. 'Outgrow the stress' posits that reinvasion pressure is determined by exotic propagule abundance and spatiotemporal availability of realized recruitment windows – the third key concept. Realized recruitment windows are periods permitting exotic recruitment from propagules and are based on the concept of 'safe sites' and current spatiotemporal invasion hypotheses, but which explicitly consider ontogenetic niche expansions in invaders. I explain that abiotic conditions over time define baseline windows of opportunity for recruitment, and that individual windows of opportunity in a given habitat are then moderated by biotic interactions with recipient communities. These interspecific interactions serve to influence growth rates and thus minimum establishment times required for plants with expanding niches to achieve the levels of abiotic tolerance needed to persist in their given environment.

In habitats where average conditions are optimal for exotic growth and survival, baseline windows of opportunity may span most of the growing season and minimum establishment times may be very short. In such cases, average reinvasion pressure should be maximized. Alternatively, in habitats where typical conditions are unsuitable for recruitment, windows of opportunity may be considerably rarer and shorter, and minimum establishment times may be substantially longer because broader tolerances would take more time to develop. In these cases, average reinvasion pressure should be minimized and biotic interactions are more likely to permit (if positive, e.g. facilitation) or preclude (if negative, e.g. competition or herbivory) recruitment in a given abiotic window of opportunity. Of course, average reinvasion pressure is a continuous variable

and could fall anywhere between these two, and short-term reinvasion pressure would vary within habitats with environmental conditions.

CHAPTER THREE – Demonstrating ontogenetic niche shifts in *Triadica*

In this chapter currently in review at the *Journal of Applied Ecology*, I began experimentally testing of the 'outgrow the stress' hypothesis by quantifying *Triadica*'s capacity for ontogenetic moisture niche expansions via three distinct studies. I performed (1) a germination experiment examining effects of soil moisture on germination over time, (2) a greenhouse experiment investigating how soil moisture and seedling age influenced seedling survival and performance, (3) a field experiment quantifying survival and performance of differently aged seedlings within a restoration site that has exhibited low average reinvasion pressure.

I found clear evidence that *Triadica* undergoes rapid ontogenetic moisture niche expansions. Moisture requirements for germination were most constrained of any life stage, with zero germination occurring in saturated or flooded soils. Seedling survival increased rapidly with age across moisture treatments and in the field. Performance also generally increased with age. Interactions of moisture and seedling age were crucial to establishing ontogenetic niche expansions statistically, and such interactions were significant for all survival metrics and all but one performance metric. Survival and performance were generally highest in intermediate moistures, modestly reduced in saturated conditions and lowest in water-limited conditions. Overall, this was clear evidence of niche expansions and demonstrated a potential mechanism by which mature *Triadica* density and average reinvasion pressure could become decoupled.

These findings have immediate and important implications for restoration and management of habitats threatened by *Triadica*, which span wetlands, grasslands and forests throughout the Gulf Coast. Specifically, I showed that density is an unreliable predictor of reinvasion but density is commonly used to guide *Triadica* management. Further, I established that cryptic opportunities are likely to exist for inexpensive and straightforward restorations of *Triadica* invaded habitats, and our detailed quantification of moisture requirements for *Triadica* recruitment will enhance climate-based estimates of *Triadica*'s average reinvasion pressure.

CHAPTER FOUR – Validating realized recruitment windows

In this chapter currently in review at *PLOS ONE*, I continued experimental validation of the 'outgrow the stress' hypothesis by testing two of its key predictions, namely that (1) recruitment will scale with temporal availability of abiotic windows, and (2) environmental factors affecting growth will influence recruitment in the same manner as they do growth during finite windows of opportunity. I did so by performing a greenhouse mesocosm experiment with field soil that quantified how duration of favorable moisture conditions prior to flood or drought stress (window duration), competition and nutrient availability influenced population-level *Triadica* recruitment in high stress environments.

In clear agreement with the first prediction, I found that window duration prior to water stress influenced abundance and performance of *Triadica* seedlings after subsequent periods of flood or drought. Support for the second hypothesis was also strong. Competition reduced both *Triadica* performance and final abundance. The type of

stress also influenced recruitment; performance was lower in drought compared to flood treatments, and stress type influenced abundance but in a less straightforward fashion with several context-dependent instances where abundances in flood treatments were lower than associated drought treatments. However, fertilization increased performance but had no effect on final *Triadica* abundance.

Overall, our results gave additional support to the 'outgrow the stress' hypothesis and demonstrated that temporal availability of favorable abiotic conditions and competition significantly impact *Triadica* recruitment in stressful environments. These findings also contribute directly to enhancing niche-based estimates of average and short-term reinvasion pressure. Further, I identified several context-dependent effects that have direct relevance to management of *Triadica* during restoration. For example, in habitats subject to drought stress, adding fertilizer in the presence of native competitors resulted in lower *Triadica* biomass than in cases of competition without fertilization.

CHAPTER FIVE – Field testing the 'outgrow the stress' hypothesis

In the capstone study of my dissertation research, I powerfully substantiated many of the key predictions of the 'outgrow the stress' hypothesis and advanced understanding of invasion in general by means of a multi-year, multi-site, replicated field experiment. Numerous studies and my previous work with *Triadica* established that propagule availability, environmental suitability and biotic interactions are important to establishment success during both invasion and reinvasion. However, the relative impacts of these factors remain unclear and likely vary among sites and over time. Moreover, these factors often interact, and extremes in one may be able to "trump" other factors in

certain circumstances. This work aimed to use the 'outgrow the stress' framework to integrate these factors and deliver greater synthetic understanding of the mechanisms governing reinvasion and the environmental thresholds likely to limit reinvasion pressure during restoration. To achieve these ends, I manipulated *Triadica* and native plant propagule availability and soil moisture within eleven replicated experimental restoration sites in southeast Texas, which represented a broad moisture gradient and were dominated by *Triadica* prior to manipulation.

'Outgrow the stress' makes several predictions regarding propagule availability, abiotic conditions and interspecific interactions. Essentially: (1) Reinvasion pressure will scale with propagule abundance but the importance of propagule will decrease as abiotic stress increases. (2) Reinvasion pressure will be a function of local environment in general and, in marginal conditions, abiotic fluctuations may permit or preclude reinvasion. (3) Competition and facilitation will influence reinvasion pressure to varying degrees depending on the environmental context but competition should generally have a net negative effect on reinvasion of all competing species.

Experimental results after three years largely corroborated these predictions. Propagule availability was the primary factor limiting reinvasion in restoration sites at the University of Houston Coastal Center and in sandier sites at Justin Hurst WMA, where soil moisture and fertility were highly favorable for *Triadica*. However, *Triadica* seed addition had a much weaker positive effect in high clay Justin Hurst WMA sites where there was relatively frequent flood stress, and adding *Triadica* seeds had no effect in the most extreme sites in Katy Prairie, where moisture availability was typically low and drought stress was often intense.

Overall, reinvasion pressure typically demonstrated a significant unimodal relationship with soil moisture and fertility. In sites subject to water stress, moisture treatments that increased or decreased the intensity of that stress had associated negative or positive effects on reinvasion pressure. Namely, wetter treatments in the flood-prone high clay Justin Hurst WMA sites exhibited significant reductions in *Triadica* reinvasion, and wetter treatments in the least drought-prone Katy Prairie site significantly increased *Triadica* reinvasion.

Interspecific interactions did not affect *Triadica* reinvasion in all sites, but native seed addition (i.e. more competition) generally reduced *Triadica* performance and significantly decreased *Triadica* survival in some sites. Interspecific interactions appeared to have considerably stronger effects on reinvasion pressure of native plants. Native prevalence was strongly negatively correlated with *Triadica* prevalence and environmental conditions that promoted *Triadica* prevalence. Treatments that increased *Triadica* reinvasion typically decreased native plant reinvasion. However, despite initial *Triadica* dominance across sites, minimal post-removal management appears to be required for successful restoration in six of eleven restoration sites.

These results powerfully support for the 'outgrow the stress' hypothesis and validate many of its specific predictions. They also provide the best documentation to date of the broad variation in (average) reinvasion pressure that may be exhibited during restorations of habitats dominated by an exotic plant. My findings further establish that we can use niche-based models to predict variation in average reinvasion pressure by considering fluctuations in both local abiotic conditions and abiotic tolerances of invaders. Such forecasts can enhance predictions of the outcomes and costs of restoration

and exotic management, which benefit ecological and economic planning. More directly, forecasts of reinvasion pressure can improve restoration and exotic management efficiency at local and landscape scales by informing optimal management strategies and/or site selection.

CHAPTER TWO

Environmental variability and ontogenetic niche shifts in exotic plants may govern reinvasion pressure in restorations of invaded ecosystems

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ABSTRACT

When restoring ecosystems dominated by exotic plants, reinvasion pressure, or the rate of new exotic recruitment following mature exotic removal, can vary broadly between similarly invaded habitats. Reinvasion pressure strongly influences restoration costs and outcomes but is difficult to predict. Ontogenetic niche shifts (changes in niche breadth or position during development) in exotic species paired with interannual variation in abiotic conditions may decouple pre-removal mature exotic density and average reinvasion pressure. Identifying such decouplings could improve restoration efficiency by informing site selection and management strategies, but requires estimates of average reinvasion pressure that mandate greater understanding of its principle drivers.

We hypothesize reinvasion pressure is predominantly driven by exotic propagule abundance and spatiotemporal availability of realized recruitment windows, which are periods of variable duration that permit exotic establishment from propagules. Realized recruitment windows are based on the 'safe sites' concept but account for ontogenetic niche shifts, and are determined by abiotic conditions and interspecific interactions with recipient communities. Biotic resistance or facilitation may increase or decrease times required for establishment by influencing exotic growth rates or altering niche availability, and may permit or preclude establishment in marginal abiotic conditions.

We discuss factors influencing reinvasion pressure, basic approaches to estimating reinvasion pressure, and potential ways to increase management efficiency under different reinvasion pressure scenarios. Accurate estimates of reinvasion pressure could improve restoration efficacy, efficiency, and predictability in ecosystems dominated by exotic plants. We argue that greater theoretical and practical consideration of reinvasion pressure and ontogenetic niche shifts are merited.

Introduction

Our ability to predict outcomes of ecological restoration is limited in habitats threatened by invasive species, which degrade ecosystems and encumber restoration efforts (Kettenring and Adams 2011). Invasive species impact native communities and ecosystem functions via direct (e.g. competition) and indirect mechanisms (e.g. altered disturbance; D'Antonio and Vitousek 1992, Yelenik et al. 2007). Invasive plant management can also impact native communities, and these non-target impacts and implications for restoration have recently received attention (e.g. Zavaleta et al. 2001, Buckley et al. 2007, Firn et al. 2008, Rinella et al. 2009, Firn et al. 2010). Impacts are predictable for specific management regimes; however, optimal management is influenced by exotic density, and management methods vary dramatically in cost (Epanchin-Niell and Hastings 2010). Exotic density also influences invader effects on communities and ecosystem functions (sensu Grime 1998). Invader and management effects are critical early in restoration due to potential impacts on community assembly and/or succession (Suding et al. 2004). Therefore, estimating exotic density over time during restoration is crucial to predicting optimal management (which drives restoration costs) and invader and exotic management impacts (which drive restoration outcomes).

This work focuses on restoring ecosystems invaded by an exotic plant species. We assume restoration begins with exotic removal and new exotic individuals will be removed before maturation, thus survival and fecundity of mature target exotics are negligible. Therefore, we can simplify traditional methods of estimating exotic density over time (via population models incorporating colonization, survival and fecundity rates) by estimating reinvasion pressure. We define reinvasion pressure (sensu Buckley et

al. 2007) as abundance and performance of exotic individuals becoming established within a habitat per management horizon after removing a dominant population of conspecifics. Simplification is desirable because quantifying site-specific model parameters and translating model outputs into management decisions are substantial tasks for professionals and beyond the scope of laypersons (Kettenring and Adams 2011). Most publically available management guidelines are based simply on mature exotic density in habitats of interest (e.g. The Nature Conservancy 2007). We argue mature exotic density can poorly predict both short-term and average (long-term mean) reinvasion pressure.

We found average reinvasion pressures varied broadly in restorations of habitats comparably invaded by Chinese tallow trees (*Triadica sebifera*). Preliminary results from experiments suggest reinvasion pressure is correlated with soil moisture but not pre-removal mature *Triadica* density (unpublished data). The literature suggests reinvasion pressure varies broadly in other species and systems. For example, Richardson and Kluge (2008) report "unpredictable and sporadic" reinvasion of *Acacia* species in South Africa, and identified correlates exclude pre-removal *Acacia* density. When exotic density correlates poorly with reinvasion pressure, restoration efforts based accordingly are prone to failure if management is inadequate or inefficiency if unnecessary management is performed (sensu Epanchin-Niell and Hastings 2010).

We provide a conceptual explanation of key factors and mechanisms governing reinvasion pressure during restorations of invaded ecosystems. We explore how predicting reinvasion pressure could enhance efficacy and efficiency of restoration projects and provide examples of particular mechanisms. Accurate estimates of reinvasion pressure would permit managers facing multiple invaded habitats to prioritize

restoration efforts where costs and exotic impacts are low, which could increase overall extent of successful restoration given limited resources. To enhance our capacity to predict restoration outcomes and costs in invaded habitats, we ask: How could average reinvasion pressure be decoupled from mature exotic plant density? How might particular quantifiable or manipulatable factors influence reinvasion pressure?

We hypothesize reinvasion pressure is decoupled from mature exotic density when abiotic tolerances of exotic plants broaden as individuals mature (ontogenetic niche expansions), and where interannual variation in abiotic conditions temporarily permit exotic recruitment in habitats typically unsuitable for recruitment. Abiotic conditions determine frequency and duration of exotic recruitment windows, which predominantly influence reinvasion pressure. Reinvasion pressure is moderated by interspecific interactions with recipient communities and is generally proportional to exotic propagule abundance. Although our examples emphasize water, our discussion of 'abiotic conditions' considers climate (temperature, water and their interactions) and resource availability, which are major factors limiting plant distributions.

Ecological contexts of invasion versus reinvasion

The literature indicates invader establishment success depends on propagule pressure, or abundance and timing of individuals introduced (Simberloff 2009), abiotic conditions or environmental filters (e.g. Kolar and Lodge 2001), and characteristics of recipient communities (e.g. Davis et al. 2000). Spatiotemporal variation in abiotic and interspecific factors are also important, e.g. as explained by 'regeneration niche' (Grubb 1977), 'safe sites' (Harper 1977), 'invasion windows' (Johnstone 1986) and 'niche

opportunity' hypotheses (Shea and Chesson 2002). Generally, abundant exotic individuals, favorable climate, weak competition or predation, and strong facilitation promote invasion success. Mechanistically, those factors influencing invasion should apply to reinvasion.

However, ecological conditions in relatively intact ecosystems as invasions begin differ from those after dominant exotic plants are removed. Ecosystems post-removal generally exhibit high resource availability, weak competition, limited native propagules and abundant exotic propagules relative to intact ecosystems. This context and/or other positive feedbacks (Suding et al. 2004) may explain why reinvasions or novel invasions often progress rapidly after invasive plant control ceases (Kettenring and Adams 2011). Fortunately, reinvasion pressure is variable but predictable.

Decoupling reinvasion pressure and exotic density

If an exotic plant's abiotic niche broadens as individuals increase in age and/or size, populations could persist in and eventually dominate habitats where conditions are typically unsuitable for recruitment but sufficiently variable to temporarily permit germination and growth to more tolerant stages. Changes in niche breadth and/or position during development are termed ontogenetic niche shifts (ONS) and occur in many plants (Figure 2.1; Eriksson 2002). ONS may permit coexistence (Grubb 1977) and influence species distributions (Eriksson 2002) and succession (Young et al. 2005). Herbivore and disease resistance can also vary ontogenetically (discussed below). We emphasize niche expansions, but ONS include niche contractions and directional shifts (Eriksson 2002). Without abiotic niche expansions, deviations from average environmental conditions

could permit recruitment but not persistence in typically unsuitable habitats. Similarly, without expansions we would not expect low average reinvasion pressure where exotics dominate because conditions promoting dominance would promote recruitment.

This scenario requires abiotic conditions suitable for exotic recruitment at some times and unsuitable for recruitment yet tolerable by older exotics (Figure 2.1) at other times. Interannual variation in abiotic conditions can trigger such transitions (Figure 2.2a-c), cause episodic recruitment (League and Veblen 2006), and influence establishment success (Bartha et al. 2003). A key consequence is exotic-dominated habitats with low average reinvasion pressures. Thus some habitats considered poor candidates for restoration could be restored relatively cheaply and easily. To identify these we must understand factors influencing reinvasion pressure.

Abiotic conditions drive reinvasion pressure by defining recruitment windows

Plants germinate and grow in discrete ranges of abiotic conditions (recruitment niche), so when environments vary temporally there may be periods when individuals can establish (Grubb 1977, Harper 1977, Johnstone 1986; Figure 2.2). These periods define "windows of opportunity" permitting recruitment. Naturally, more opportunities and time to develop broader tolerances increase establishment success. Therefore, window frequency and duration should strongly influence reinvasion pressure. Both vary by species and habitat and temporally within habitats due to interannual variation. Conditions during windows affect reinvasion pressure by influencing performance and potentially establishment success if size influences tolerances (Figure 2.1). By defining

frequencies and durations of recruitment windows and influencing performance, we expect abiotic conditions drive reinvasion pressure when exotic propagules are abundant.

Recruitment windows may span entire growing seasons where abiotic conditions are highly suitable for the invader (Figure 2.2b). Here average reinvasion pressure is maximized and recruitment may fail only when interannual variation is extreme. Conversely, average reinvasion pressure is minimized where typical conditions are unsuitable for exotic recruitment (Figure 2.2a). However, large deviations from average conditions (e.g. droughts, floods) may provide rare recruitment windows that permit exotics with expanding niches to germinate and reach stages or sizes tolerant of average conditions. Subsequent windows could permit dominance when propagules are limiting. We hypothesize this mechanism underlies the strongest decouplings of average reinvasion pressure from mature exotic abundance.

Average reinvasion pressure may be moderate where typical conditions are near an exotic's limits for recruitment (Figure 2.2c). In borderline conditions, interannual variation could more frequently permit or preclude recruitment, causing intermittent and possibly shorter recruitment windows. Marginal abiotic conditions could also reduce exotic performance and/or survival, potentially moderating reinvasion pressure even if windows occur annually.

Propagule availability fuels reinvasion

Simberloff (2009) reviewed mounting evidence that propagule pressure is centrally important to establishment and spread phases of invasions. He suggests increased colonizer abundances and frequencies of colonization events promote

establishment by dampening effects of demographic and environmental stochasticity, respectively. Exotic propagule pressure may even supersede physical environment in determining invasion success in some systems (Von Holle and Simberloff 2005).

When restoring invaded ecosystems, initial exotic propagule abundance varies but is generally high, and propagules remain present until they die or become juveniles subject to management. Sexual invaders often produce more seeds than could establish in available space due to self-thinning, and these "supersaturated" seedbanks may fuel high reinvasion pressure for years despite recurring management (e.g. Healy and Zedler 2010). We suggest supersaturated seedbanks are common for abundant, fecund invaders and differences in exotic propagule abundance beyond saturation have little impact on reinvasion pressure because spatial carrying capacity likely depends more on abiotic conditions.

Nevertheless, recruits cannot exceed propagules, so propagule availability may determine reinvasion pressure when propagule density is below spatial saturation. Even if supersaturated, propagule density could affect reinvasion pressure if suboptimal abiotic conditions reduce germination or survival rates. Thus we hypothesize reinvasion pressure is generally proportional to propagule availability. Reinvasion pressure may decrease rapidly if exotic propagules are short-lived, or if ecological conditions (e.g. seed predators; Richardson and Kluge 2008) or management (e.g. burning; Firn et al. 2008) reduce their viability. When invaders cannot store propagules, external propagule pressure likely heavily influences reinvasion pressure. Exotic propagule availability and longevity, and factors influencing propagule viability may impact reinvasion pressure.

Interspecific interactions moderate reinvasion pressure

Mack et al. (2000) suggest communities vulnerable to invasion exhibit: vacant niches, few biotic constraints, low species richness, and/or disturbance. Essentially, these focus on biotic resistance – how strongly natural enemies or competitors negatively impact invaders – with niche saturation, enemy release, community structure, and reduced native abundance proposed as key mechanisms. Positive impacts of facilitation are also recognized (e.g. Maron and Connors 1996). Interactions among these factors and resource availability, and their spatiotemporal variation are crucial to invasion success (Johnstone 1986, Davis et al. 2000, Shea and Chesson 2002).

In our context, one generally expects weak biotic resistance. By definition, after removal of dominant exotic plants, habitats exhibit: high space and light availability, relatively low plant abundance, disturbance of some type, and often reduced species richness and niche saturation. If enemy release influenced invasion, localized exotic removal would not introduce coevolved natural enemies and should have little impact on native herbivores or pathogens. Thus we expect biotic resistance generally has little impact on reinvasion pressure when resources are available and competitors are scarce.

However, many restoration techniques alter characteristics of recipient communities. Introducing native competitors or biocontrol agents can bolster biotic resistance following exotic removal (Funk et al. 2008, Kettenring and Adams 2011). Introductions may not preclude reinvasion but may reduce reinvasion pressure by decreasing exotic survival or performance. Depending on abiotic conditions, reducing exotic performance could preclude establishment during some recruitment windows (discussed below).

Natural enemies may influence reinvasion pressure, particularly when exotic plants' defensive capabilities strengthen during development. A meta-analysis by Barton and Koricheva (2010) found that herbivore defenses (especially chemicals) increase through ontogeny, especially rapidly during the seedling stage. Comparably, plants are generally more susceptible to disease early in development, with pathogen resistance developing gradually or at major life cycle transitions (reviewed by Develey-Riviere and Galiana 2007). Interannual variation in natural enemy abundances paired with "windows of vulnerability" early in plant development may produce temporal variation in exotic recruitment success, and could also decouple average reinvasion pressure from abundance of mature exotics not subject to enemy release.

Synthesis: realized recruitment windows and 'outgrow the stress' hypothesis

We posit exotic management is most efficient when planned according to timing of realized recruitment windows (Figure 2.2j-l). If plant size, which is a function of age and growth rate, determines physiological tolerances (Blum et al. 1997, Kunstler et al. 2009), all factors governing growth rate during recruitment windows will influence recruitment success. Our 'outgrow the stress' hypothesis holds that: (1) Age and ecological conditions determine plant size, which determines a species' abiotic tolerances that ultimately limit its success during recruitment windows when its propagules are abundant. (2) Availabilities of propagules and realized recruitment windows determine recruitment success over time, which determines reinvasion pressure.

Caveat: Net positive interspecific effects could reduce establishment times (unlike Figure 2.2g-l). We doubt this is common and note most modes of facilitation are

considered elsewhere in our model: pollination and dispersal influence propagule availability, and theoretical recruitment windows consider microclimates produced by nurse plants. Very strong facilitation, e.g. via mycorrhizae, could void this assumption.

Conclusions and recommendations

Our conceptual model explains potential mechanisms underlying variable reinvasion pressure in restorations of habitats dominated by exotic plants. Average reinvasion pressure may be decoupled from mature exotic density when interannual variation in abiotic conditions (Figure 2.2a-c) permits exotics exhibiting ontogenetic niche expansions (Figure 2.1) to dominate habitats where their average recruitment success is relatively low. Abiotic conditions drive reinvasion pressure by defining availability of recruitment windows (Figure 2.2d-i) and influencing exotic performance. Reinvasion pressure is generally proportional to exotic propagule abundance, but may plateau at spatial saturation. Practitioners can most control biotic resistance, which moderates reinvasion pressure by influencing exotic survival and performance, and may preclude exotic recruitment in some situations (Figure 2.2j-l). Ultimately, spatiotemporal availability of exotic propagules and realized recruitment windows determine reinvasion pressure.

Without reliable predictors, sound estimates of average reinvasion pressure require sizeable but attainable amounts of data. Basic knowledge of the target exotic plant's abiotic and functional niches; capacity for niche shifts; germination, growth and reproductive rates and strategies; phenology; propagule longevity; natural enemies; and responses to particular exotic control methods is essential. For problematic and well-

studied invaders, this information is likely common knowledge among average managers or attainable via agricultural extension. For less-studied invaders, sufficient information for rudimentary estimates is likely attainable through agricultural extension. Necessary information may be unavailable for emerging invaders, but data on closely related species may be suitable. If not, we suggest estimates via repeated surveys or pilot studies (see below), and adaptive management where estimates are unattainable or unreliable.

Data on environmental conditions, interannual variability, disturbance regime, and natural enemies within candidate habitats are also necessary. This could come from historic climate and/or disturbance records, soil maps, experience, or could be inferred from extant species' requirements. One could estimate average reinvasion pressure directly via repeated surveys of exotic germination, survival and performance in candidate restoration sites, or preferably via pilot experiments under environmental conditions expected following exotic removal.

Where invaders are well-studied or resources permit in situ research, reliable estimates of reinvasion pressure are highly realistic and practical. Where invaders are less-studied and research capacity is low, coarser estimates are still realistic but may only be practical if existing management methods or decision making tools are deficient. Developing estimates is likely impractical for independent managers without substantial preexisting data for their system (e.g. in understudied regions) or access to it (e.g. in developing regions). Reliable estimates of average reinvasion pressure can guide management to enhance restoration efficacy and efficiency (see Implications). Reinvasion pressure is a general, quantifiable metric that provides a useful decision

making context and may guide management strategies and site selection wherever invasion has already occurred.

Implications for Practice

- Where average reinvasion pressure is high: Emphasize management that reduces exotic propagule abundance or viability. Avoid native introductions until need for destructive management diminishes.
- Where moderate: Avoid destructive management and increase biotic resistance early via native introductions. Reduce exotic propagule abundance only when inexpensive or seedbanks are long-lived.
- Where low: Utilize management strategies responsive to episodic recruitment pulses rather than annual management. Prioritize these habitats.
- Generally: Utilize adaptive management strategies that accommodate fluctuations in exotic recruitment so exotic control is always commensurate with reinvasion pressure.

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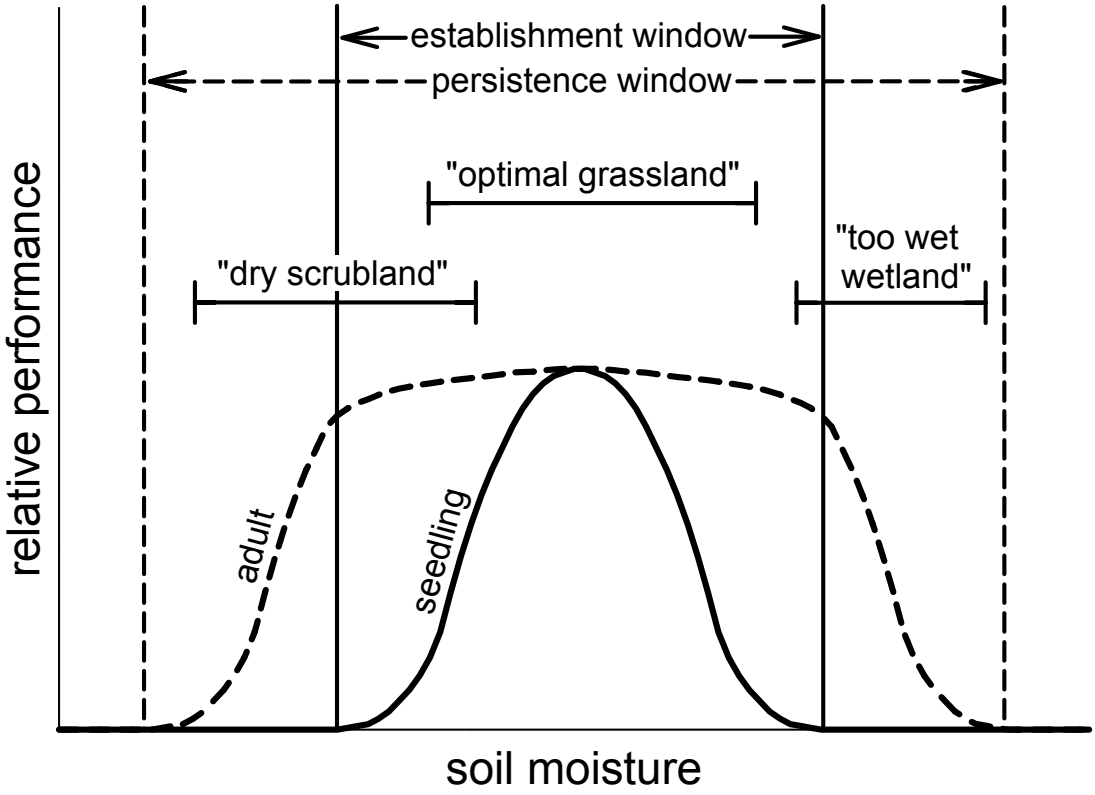

Figure 2.1. Adults of a hypothetical species (dashed curve) tolerate a broader range of moisture than seedlings (solid curve). Ontogenetic niche expansions like this demonstrate how adults may persist in conditions unsuitable for their establishment. Horizontal bars represent moisture ranges for three hypothetical habitats; their overlaps with the establishment window suggest the species can colonize the wetland rarely, the scrubland occasionally, and the grassland always.

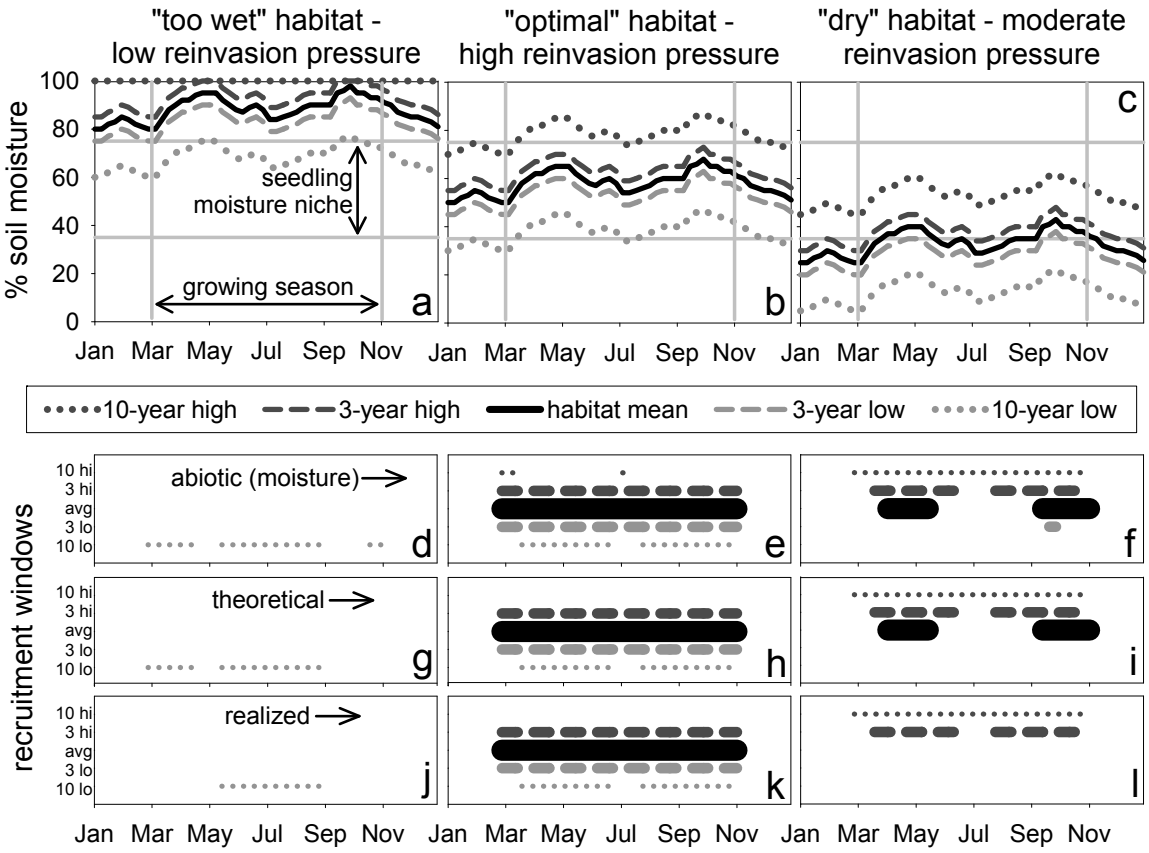

Figure 2.2. Contours in panels a - c demonstrate ranges and frequencies of soil moisture fluctuations in three hypothetical habitats exhibiting interannual variation. Horizontal lines in panels d - l represent periods, weighted by frequency, when moisture conditions could permit recruitment of a hypothetical plant species with an expanding moisture niche (recruitment windows). For simplicity, we assume seedling performance is equal across the moisture niche, mortality is instantaneous outside the moisture niche, and interspecific interactions produce a universal net negative effect on performance. Abiotic recruitment windows (d - f) occur when abiotic conditions are suitable for germination and seedling growth – here when moisture contours (a - c) fall within the moisture niche and growing season. However, niche expansions take time. Theoretical recruitment windows (g - i) occur when abiotic windows persist long enough for seedlings to germinate and develop tolerances to subsequent conditions (to become established) based

on individuals' physiological growth rates – here minimum establishment time is six weeks, so only abiotic windows ≥6 weeks are theoretical windows. However, biotic interactions influence seedling performance and thus establishment time. Realized recruitment windows (j - l) occur when abiotic windows are long enough to permit establishment given local abiotic and biotic conditions – here biotic resistance halves growth rate and doubles establishment time, so only abiotic windows ≥12 weeks are realized windows. In the "too wet" habitat (a), recruitment is episodic and may succeed only during 10-year lows (d, g, j), so average reinvasion pressure is low. In the "optimal" habitat (b), recruitment is typical because suitable conditions span the growing season except during 10-year extremes (e, h, k), so average reinvasion pressure is high. In the "dry" habitat (c), recruitment is intermittent and may succeed only in relatively wet years (f, i, l), so average reinvasion pressure is moderate; notably, here biotic resistance precludes recruitment in average years (i versus l).

CHAPTER THREE

Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavorable but variable environments and can be exploited to streamline restoration

In review at *Journal of Applied Ecology*

Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavorable but variable environments and can be exploited to streamline restoration

ABSTRACT

Reinvasion pressure is the rate of new exotic recruitment following mature exotic removal and it can vary broadly among similarly invaded habitats. Reinvasion pressure drives restoration outcomes and costs but is difficult to predict and poorly understood. *Triadica sebifera* (Chinese tallow tree) is a major invader demonstrating broad variation in average reinvasion pressure. We hypothesize this variation arises from differences in moisture regimes among habitats, which drive differences in *Triadica* recruitment but are masked because *Triadica* exhibits ontogenetic niche expansions (increases in niche breadth during development) that enable dominance in habitats where average recruitment success is low.

We began testing this hypothesis by quantifying *Triadica*'s capacity for ontogenetic moisture niche expansions. We performed greenhouse experiments examining how soil moisture affects germination likelihood and timing and how soil moisture and seedling age influenced seedling survival and performance, plus a field experiment quantifying survival and performance of differently aged seedlings within a restoration site that has exhibited low average reinvasion pressure.

Moisture requirements for germination were most constrained of any life stage. Zero germination occurred in saturated or flooded soils despite high seedling survival in

comparable conditions. Germination timing varied among suitable moisture treatments.

Seedling survival increased rapidly with age across moisture treatments and in the field. Aboveground biomass increased with age; tissue-specific performance metrics did as well but reflected seed provisioning, age-specific carbon allocation preferences, or tissue shedding for survival. Crucial moisture*age interactions that signify ontogenetic niche expansions were significant for all survival metrics and all but one performance metric.

Survival and performance were generally highest in intermediate moistures, modestly reduced in saturated conditions and lowest in water-limited conditions.

Synthesis and applications. Our results show *Triadica* exhibits rapid ontogenetic moisture niche expansions which could decouple mature *Triadica* density and average reinvasion pressure. Therefore, density is an unreliable predictor of reinvasion but is commonly used to guide *Triadica* management, and cryptic opportunities exist for inexpensive and straightforward restorations. Reliable moisture niche-based estimates of *Triadica*'s average reinvasion pressure are feasible and may improve restoration efficacy and efficiency by informing site selection and optimal management strategies.

INTRODUCTION

Invasive species degrade ecosystems and impede restoration worldwide, particularly in habitats they dominate (Kettenring and Adams 2011). When restoring ecosystems dominated by an exotic plant, reinvasion pressure is the rate of new exotic recruitment following mature exotic removal and it can vary broadly between similarly invaded habitats (Buckley et al. 2007). Reinvasion pressure is crucial to restoration outcomes and costs because plant density moderates invader effects on communities and ecosystem functions (Grime 1998) and influences required management methods, which have manifold non-target impacts (Rinella et al. 2009) and vary widely in cost (Epanchin-Niell and Hastings 2010). Reinvasion pressure is difficult to predict, but accurate estimates are feasible and may improve restoration efficacy and efficiency by informing site selection and optimal management strategies (Gabler and Siemann 2012). Despite broad implications for applied ecology, reinvasion pressure and the mechanisms of its variation are poorly understood (Kettenring and Adams 2011).

Triadica sebifera (Chinese tallow tree) is a major invader in the southeastern United States with broad variation in average reinvasion pressure during restorations of habitats it dominated (Donahue et al. 2006; Gabler and Siemann, unpublished data). We hypothesize this variation arises because *Triadica* exhibits ontogenetic niche expansions (increases in niche breadth during development) that enable individuals to persist in habitats where moisture regimes range from being frequently, highly suitable for *Triadica* recruitment to being rarely, marginally suitable. If so, we theorize abiotic variation among invaded habitats drives differences in recruitment success that underlie observed

variation in average (long-term mean) reinvasion pressure (Gabler and Siemann 2012). Whether recruitment is regular or episodic, ontogenetic niche expansions would permit high densities of *Triadica* to develop over time that mask underlying abiotic variation and thus average reinvasion pressure. We refer to the phenomenon where average reinvasion pressure is relatively low despite high mature exotic density as 'density-reinvasion decoupling.' This work begins testing this hypothesis by quantifying *Triadica*'s capacity for ontogenetic moisture niche expansions.

Ontogenetic niche expansions are increases in niche breadth during an individual's life (Parrish and Bazzaz 1985, Gabler and Siemann 2012; Figure 2.1); niche contractions (Quero et al. 2008) and directional shifts also occur (Eriksson 2002). Ontogenetic changes in plant abiotic requirements may permit coexistence (Grubb 1977) and can influence species distributions and population dynamics (Parrish and Bazzaz 1985, Eriksson 2002, Donohue et al. 2010), plant-plant interactions (Miriti 2006, Quero et al. 2008) and succession (Young et al. 2005). However, ontogenetic niche changes in plants are understudied, rarely used to explain reinvasion and seldom considered in practice, despite their relevance to population and community ecology and a review by Young, Peterson and Clary (2005) emphasizing their importance to restoration and scarcity of applicable research.

Ontogenetic niche expansions can explain density-reinvasion decoupling, but we posit that short-term reinvasion pressure is determined by exotic propagule abundance and spatiotemporal availability of realized recruitment windows (Gabler and Siemann 2012). Realized recruitment windows are based on 'safe sites' (Harper 1977) and coexistence (Chesson 2000) and invasion hypotheses that stress spatiotemporal variation

(Davis et al. 2000, Shea and Chesson 2002) but emphasize ontogenetic niche expansions. Realized windows are periods of variable duration that permit recruitment of exotics with expanding niches and are fundamentally defined by abiotic conditions. Thus, spatiotemporal (e.g. interannual) variation in abiotic conditions within habitats is crucial to reinvasion pressure.

We emphasize *Triadica*'s moisture niche and moisture variation among habitats because we expect water is particularly important to *Triadica* recruitment and persistence. Temperature defines *Triadica*'s northern limits, but water regime is crucial to its local distribution and can vary considerably on small spatial scales in its introduced range (Bruce et al. 1997). Preliminary results from experimental restorations of *Triadica*-dominated sites suggest reinvasion pressure correlates with soil moisture but not pre-removal *Triadica* density (Gabler and Siemann, unpublished data). In other systems, interannual variation in precipitation can influence seed production (Perez-Ramos et al. 2010) and establishment success (Bartha et al. 2003) and cause episodic recruitment (Crawley 1990), which are all important to reinvasion.

If ontogenetic niche expansions in *Triadica*'s moisture tolerance underlie observed variation in its reinvasion pressure, we may be able to predict short-term and average (long-term mean) *Triadica* recruitment within particular habitats by emphasizing climate forecasts or average abiotic conditions, respectively. Such predictions would be extremely valuable decision-making tools in planning and executing restoration and/or exotic removal in habitats invaded by *Triadica*, and this approach should be applicable for other species and systems. Great potential to avoid unnecessary management lies in our capacity to identify density-reinvasion decouplings. Generally, accurate estimates of

reinvasion pressure could improve restoration efficacy, efficiency, and predictability in any ecosystem dominated by exotic plants.

We investigated whether *Triadica* undergoes ontogenetic niche expansions by performing three experiments quantifying breadths of moisture tolerance at different stages early in *Triadica* development. If *Triadica*'s moisture niche expands ontogenetically, its germination niche will be most constrained and older seedlings will survive across a broader range of moisture conditions and exhibit higher performance than younger seedlings. To better understand how ontogenetic patterns of moisture tolerance in an important invasive plant and moisture patterns in recipient habitats may influence reinvasion pressure, we ask: (i) What are *Triadica*'s moisture requirements for germination and seedling survival and growth? (ii) Does *Triadica* undergo ontogenetic niche expansions? If so, how and when do its moisture tolerances change during development? (iii) Can niche expansions explain observed *Triadica* recruitment patterns? That is, can seedling age influence survival of *Triadica* in habitats exhibiting very low average reinvasion pressure?

METHODS

Focal species and study site

Chinese tallow tree [*Triadica sebifera* (L.) Small, Euphorbiaceae; synonym *Sapium sebiferum;* '*Triadica*' throughout] is an invasive exotic species in the southeastern United States naturalized from Texas to Florida and northward from Arkansas to North Carolina and in California (Bruce et al. 1997, Aslan 2011). *Triadica*

aggressively displaces native species in grasslands (including imperiled coastal prairies), wetlands and forests to form monocultures in as little as two decades (Bruce et al. 1997, Harcombe et al. 1999). *Triadica* demonstrates competitive superiority arising from high growth rates (Lin et al. 2004), prolific seed production (Renne et al. 2000), broad abiotic tolerances (Jones and McLeod 1989, Butterfield et al. 2004) and low herbivore loads (Siemann and Rogers 2003a). Seeds require oscillating temperatures characteristic of exposed soil to break dormancy, which promotes *Triadica* germination in disturbed conditions (Nijjer et al. 2002, Donahue et al. 2004, 2006). Established *Triadica* seedlings have broad moisture tolerances (e.g. Hall and Harcombe 1998, Butterfield et al. 2004), but moisture requirements for *Triadica* germination and early development have not been quantified and are crucial to our framework.

We performed our field experiment within a 1.2 ha experimental restoration site in Justin Hurst Wildlife Management Area (JHWMA) near Jones Creek, Texas, USA (28.959502 N, -95.461348 W). JHWMA is ~100 km south of Houston and spans 4,835 ha of grasslands and wetlands characteristic of the United States Western Gulf Coastal Plain ecoregion. Land is nearly level and poorly drained with elevation generally <2 m above mean sea level. Average annual temperature is 20.8°C, and average annual rainfall is 1320 mm with 60% between April and September. Study area soils are expansive Pledger (85%) and Brazoria Clay (10%) vertisols (very-fine, smectitic, hyperthermic Typic Hapluderts) with 60-80% clay content (classification follows USDA/NRCS Soil Taxonomy).

The restoration site encompasses a seasonally-flooded freshwater depressional wetland that was dominated by closed-canopy *Triadica* woodland with minimal native

understory before restoration began in 2006. In 2010 the study area had an understory dominated by *Carex oxylepis* Torr. & Hook. (Cyperaceae; 55% cover) with various other forbs (13%) and grasses (5%) and an open, low-statured overstory of woody *Sesbania drummondii* (Rydb.) Cory (Fabaceae; 31% canopy cover). *Triadica* saplings contributed only 1.8% canopy cover and no seedlings were observed. Since restoration began, *Triadica* has remained exceedingly rare site-wide including within unmanaged areas and *Triadica* seed addition plots (Gabler and Siemann, unpublished data). *Triadica* reinvasion pressure has been substantially lower here than in any other documented restoration of *Triadica*-dominated habitat.

Germination experiment

The germination experiment quantified impacts of soil moisture and source tree on germination likelihood and timing. The full factorial design used 46.6 ml polystyrene vials (25 mm wide × 95 mm tall) filled with ~34 ml field soil from JHWMA with six moisture treatments, ten source trees and eight replicates per combination (n = 480 vials). In June 2010 we planted two washed *Triadica* seeds (see Appendix 3.S1 in Supporting Information) collected in 2009 in each vial and immediately imposed moisture treatments: (i) 'drought' – 15 ml water added (watered) every 28 days, vials bottom draining; (ii) 'dry' – watered weekly, bottom draining; (iii) 'field capacity' – watered daily, bottom draining; (iv) 'subsurface saturation' – watered daily, side draining so the top 35 mm of soil drained and bottom 35 mm remained saturated; (v) 'saturated' – watered daily, side draining so all soil remained saturated without standing water; (vi) 'flooded' – "topped off" daily and undrained so 20-25 mm (depending on evaporation)

standing water remained. Moisture treatments here and below mimic the range of typical moisture conditions in sites where juvenile and mature *Triadica* are commonly observed.

We housed vials in a climate controlled greenhouse under natural light with day temperatures of 34-36°C and night temperatures of 23-25°C, which approximates summer in southeast Texas. *Triadica* germination peaks in spring but can occur throughout the growing season in dry to temporarily flooded soils. We watered, maintained drainage and surveyed vials daily. We removed germinated seeds and smoothed soil surfaces immediately to maximize microclimate consistency within vials. After 60 days we observed zero germination (in vials and independent trials under optimal conditions), presumed *Triadica* seeds utilized were unviable and planted two or three additional seeds collected in 2008 from one of eight novel source trees in each vial. We continued as before for 91 days and concluded experimentation in November 2010 after 14 consecutive days with no germination. We report germination timing based on the second planting but germination likelihoods based on total seeds from both plantings. We used repeated measures ANOVA (aov in R 2.13; R Foundation for Statistical Computing, Vienna, Austria) to test effects of soil moisture, source tree, time and their interactions on *Triadica* germination likelihood. Error was partitioned across subjects (vials) for factors excluding time and within subjects for factors including time. We used Holm-Bonferroni adjusted pairwise t-tests to identify differences between treatments means.

Greenhouse experiment

The greenhouse experiment quantified survival and performance of differently

aged *Triadica* seedlings along a moisture gradient. The unbalanced full factorial design used 2.8 L pots with six moisture treatments, six seedling age treatments and 5-10 replicates per treatment combination (n = 287 pots). In June 2008 we added washed (see Appendix 3.S1) *Triadica* seeds from each of 21 source trees to separate trays of Metro-Mix® (Sun Gro Horticulture, Washington, USA) for germination. We watered trays daily and housed them in a climate controlled greenhouse under natural light with day temperatures of 29-31°C and night temperatures of 19-21°C, which approximates spring in southeast Texas. We transplanted newly germinated seedlings into 2.8 L tapered square plastic Treepots (36 cm tall, 6-10 cm diameter; Stuewe & Sons, Oregon, USA) filled with ~2 L field soil collected from JHWMA, assigned each an age and moisture treatment and recorded its source tree.

We established six age treatments by exposing seedlings to identical well-drained and well-watered conditions for 1, 7, 14, 28, 42 or 56 day(s) before imposing moisture treatments. We established six soil moisture treatments by manipulating pot drainage and thrice weekly watering as follows: (i) 'drought' (DRT) – well-drained, watered as needed to maintain soil moisture at 25% field capacity by mass (see Appendix 3.S2); (ii) 'dry' (DRY) – well-drained, watered as needed to maintain 50% field capacity; (iii) 'field capacity' (CAP) – well-drained, well-watered; (iv) 'subsurface saturation' (WET) – well-watered, pots inside non-draining containers so the top 10 cm of soil drained and bottom 16 cm remained saturated; (v) 'saturated' (SAT) – pots sealed with drain holes 1 cm above the soil surface and topped off so all soil remained saturated with minimal standing water; (vi) 'flooded' (FLD) – pots sealed and topped off so 8-10 cm of standing water (depending on evaporation) remained. We synchronized when seedlings were exposed to

moisture treatments as much as possible by assigning germinants to age treatments sequentially from oldest to youngest. The three youngest age treatments have fewer replicates than older age treatments because seed viability was low.

We surveyed seedling height, leaf count and basal stem diameter at onset of moisture treatments and 56 days later, and surveyed survival at least thrice weekly. After final surveys we harvested aboveground biomass of all survivors and root biomass from survivors in the 56 days age treatment. Biomass samples were oven-dried at 70°C for 48 h and weighed. We used survival analyses to examine dependence of seedling survival time on experimental treatments. We fit right-censored survival data with parametric accelerated failure time models (survreg in R) utilizing Weibull distributions. We included moisture treatment (categorical) and seedling age (continuous) as covariates and used likelihood ratio tests to determine whether survival time depended on moisture, age and/or their interaction. We also performed these analyses with source tree as a covariate. This marginally improved our models but did not affect significance of other factors and source tree was insignificant [χ^2 (21 d.f.) = 26.09, P = 0.20], so we excluded source tree from further analyses. As an alternative to survival analysis because most seedlings survived, we fit number of days survived using a generalized linear model (GLM; glm in R) with a Poisson distribution and used analysis of deviance (ANODEV, a form of likelihood ratio testing; anova in R) with chi-square tests to evaluate whether experimental treatments and/or their interactions influenced survival time.

To examine effects of experimental treatments on seedling performance we fit performance data with GLM's because mortality variation among treatments and/or experimental design artifacts produced unbalanced sample sizes. We used ANOVAs (aov

in R) to test whether soil moisture, seedling age (categorical), source tree and/or their interactions influenced absolute changes in seedling height, leaf abundance and stem diameter (square root transformed), final above- and belowground biomass (both $\log_e$ transformed), and root:shoot ($\log_e$ transformed). We also fit GLM's and used ANOVAs to test dependence of relative [(ln final – ln initial) / ($t_1 - t_0$)] performance variables and age-scaled aboveground biomass on experimental treatments and their interactions. These results were qualitatively equivalent to their counterparts based on absolute or unscaled data and are not shown.

Field experiment

The field experiment quantified survival and performance of differently aged *Triadica* seedlings under field conditions. We used a simple one-way design by transplanting *Triadica* seedlings from six age treatments with 10 replicates into the JHWMA restoration site (n = 60 seedlings). In June 2010 we germinated *Triadica* seeds as above in the same greenhouse conditions as the germination experiment. We established six age treatments by transferring new germinants to pots of JHWMA soil and exposing them to identical well-drained, daily-watered conditions for 1, 13, 20, 34, 48 or 62 day(s) prior to transplantation. To avoid restricting belowground growth we used 6.2 L tapered square Treepots (Stuewe & Sons) for 62 and 48 days treatments, 2.8 L Treepots for 34 and 20 days treatments, 1.75 L round pots for the 13 day treatment and 115 ml Cone-tainers™ (Stuewe & Sons) for the 1 day treatment. We moved all seedlings except the 1 day treatment outside into partial shade to "harden off" for 7 days prior to transplantation.

On 17 September 2010 we measured seedling height and leaf abundance and transplanted seedlings with their soil monoliths into the JHWMA restoration site along a randomized 6 × 10 grid with 1 m spacing. To minimize environmental heterogeneity we removed vegetation within 10 cm of seedlings and clipped vegetation within 4 m to ~5 cm in height. Flooding occurred in late September only (~15% of experiment duration). Given average rainfall, the site is intermittently flooded (~75% of the time) year-round (*personal observation*). We surveyed seedling survival 13 days post-transplantation and approximately weekly thereafter. Turbid standing water prevented a survival survey 6 days post-transplantation, so we measured depth at grid nodes, confirmed depth was independent of age treatments (ANOVA, $F_{5,54} = 1.32$, $P = 0.27$) and excluded depth from further analyses. After 56 days we measured seedling height and leaf abundance and harvested, dried and weighed aboveground biomass of all survivors. Our timing was unusual but realistic (*Triadica* can germinate February-November in Texas). This experiment was a test of mechanism requiring exposure of age classes that would not typically co-occur to identical, realistic conditions. Our methods achieved this end, thus timing was inconsequential. Analyses followed the same approach as in the greenhouse experiment.

RESULTS

Germination likelihood and timing

Germination likelihood depended on moisture treatment, source tree, time and all interactions (Table 3.1). Final germination percentages in subsurface saturation, field

capacity and dry treatments were not significantly different but were higher than in drought, saturated and flooded treatments (Figure 3.1). Mean time to germination was 31.4 days but timing varied by moisture, with percent germination in drought and dry treatments plateauing earlier (~30 days) than in intermediate moisture treatments (~70 days; Figure 3.1). Germination timing also depended on source tree but followed no apparent pattern.

Greenhouse survival and performance

Survival time in survival analysis depended on soil moisture [χ^2 (5 d.f.) = 116.65, $P < 0.001$], seedling age [χ^2 (1 d.f.) = 28.80, $P < 0.001$] and moisture*age interaction [χ^2 (5 d.f.) = 31.51, $P < 0.001$], which signifies an ontogenetic niche shift. This was supported by ANODEV of days survived, which showed that moisture, age, source tree and all interactions thereof influenced survival time (Table 3.2). Uncensored survival time averaged 51.6 days overall and was highest in intermediate and saturated moisture treatments, slightly reduced in the flooded treatment and lowest in water-limited treatments (Figure 3.2). Survival time increased rapidly with age, although there was a non-significant decrease among the oldest seedlings in the driest treatment (Figure 3.2). Survival likelihoods followed similar patterns (Table 3.S1).

All metrics of seedling performance depended on soil moisture and seedling age, and source tree affected changes in height and stem diameter but not leaf count nor final aboveground biomass (Table 3.2). The moisture*age interaction influenced aboveground biomass and changes in height and leaf count but not stem diameter (Table 3.2). Every performance metric was significantly higher in intermediate moisture treatments than in

water-limited treatments; performance in saturated treatments was generally in between (Figure 3.3; Tables S1 and S2). Aboveground biomass increased with age, but increases in height and leaf abundance were highest among seedlings aged 1 and 42 days, and increases in stem diameter were highest among seedlings aged 14 and 28 days (Table 3.S1).

Root biomass among seedlings aged 56 days was influenced by soil moisture ($F_{5,41} = 7.63$, $P < 0.001$) but neither source tree ($F_{8,41} = 0.74$, $P = 0.65$) nor moisture*tree ($F_{12,41} = 1.93$, $P = 0.11$). Root:shoot depended on source tree ($F_{8,41} = 4.41$, $P = 0.006$) but was independent of moisture ($F_{5,41} = 2.43$, $P = 0.08$) and moisture*tree ($F_{12,41} = 1.59$, $P = 0.19$). Root biomass followed prior moisture patterns: lowest in DRT (182 mg) and DRY (237 mg), highest in CAP (789 mg), WET (609 mg) and SAT (591 mg), and reduced in FLD (401 mg). Root:shoot ranged from 0.39 to 0.61 among source trees and there was an insignificant trend for it to decrease as moisture increased (from 0.87 in DRT to 0.43 in FLD).

Field survival and performance

Average survival time was 30.9 days and 23 of 60 *Triadica* seedlings (38.3%) survived until final surveys 56 days post-transplant. Seedling age influenced survival time in survival analysis [χ^2 (1 d.f.) = 66.69, $P < 0.001$] and ANODEV of days survived [χ^2 (5 d.f.) = 502.48, $P < 0.001$, McFadden's pseudo $R^2 = 0.489$]. Survival increased with age less rapidly than in the greenhouse (Figure 3.4; Table 3.S3). All seedlings aged 1 or 13 day(s) died within 26 days. Only 25% of seedlings aged 20 or 34 days survived, but 80% survived among seedlings aged 48 days. All seedlings aged 62 days survived.

Seedling age influenced aboveground biomass ($F_{3,22} = 3.89$, $P = 0.025$, pseudo $R^2 = 0.219$) and change in leaf count ($F_{3,22} = 5.21$, $P = 0.009$, pseudo $R^2 = 0.081$) but not change in height ($F_{3,22} = 1.29$, $P = 0.31$, pseudo $R^2 = 0.015$). Biomass increased with age as in the greenhouse, but most seedlings lost leaves under field conditions and older seedlings lost more (Table 3.S3).

DISCUSSION

Reinvasion pressure is crucial to restoration outcomes and costs, but it can vary broadly among habitats invaded by the same plant species and is difficult to predict (Buckley et al. 2007, Kettenring and Adams 2011). Ontogenetic niche expansions can promote density-reinvasion decoupling that masks average reinvasion pressure and has important implications for restorations of invaded ecosystems (Gabler and Siemann 2012). Our results clearly show that *Triadica sebifera* (Chinese tallow tree), a major invader in North America, exhibits rapid ontogenetic expansions in its moisture niche. This may enable *Triadica* seedlings to persist within habitats where conditions are typically unsuitable for recruitment, thus permitting mature exotic density and average reinvasion pressure to become decoupled over time.

Triadica survival increased rapidly with seedling age in the greenhouse and field. Biomass also increased with age, but tissue-specific performance metrics had more complex relationships with age that likely reflected seed provisioning, preferential carbon allocation in different developmental stages, or tissue shedding for survival. Seed provisioning could explain large increases in some treatments among the youngest

seedlings, which should benefit most from considerable nutritional stores in *Triadica* seeds. Seed provisioning offered little benefit in FLD treatments, where performance of seedlings aged 1 day was generally lowest (Table 3.S1). Whether seedlings had any emergent leaves appears crucial to success in flooded conditions. In FLD pots, depth reached ~80 mm between watering, and only 38% of seedlings initially ≤80 mm tall survived, but 100% of seedlings initially >80 mm tall survived. In the field experiment, zero seedlings aged 1 or 13 days survived to harvest. We doubt transplant shock was a factor because our well-established transplantation protocols yield >95% survival. Generally, greenhouse survival and performance were highest in intermediate soil moisture treatments, modestly reduced in saturated treatments and lowest in drier treatments.

Our findings support the hypothesis of Parrish and Bazzaz (1985) that germination niches are most specific for species with seed dormancy. Donohue et al. (2010) explain that narrower germination niches (i.e. ontogenetic niche expansions) may restrict spatial distribution but reduce seedling mortality by promoting germination under optimal conditions. Abrupt attenuation of *Triadica* germination in moisture conditions suboptimal for young seedlings suggests a selective cuing mechanism. Specific germination cuing may enable *Triadica* to select favorable conditions within temporally variable landscapes across a broad geographic range (Donohue et al. 2010) and could contribute to its invasive success.

The crucial moisture*age interaction means moisture effects depended on seedling age and indicates ontogenetic change in moisture tolerance. Extreme moisture conditions reduced survival and performance among older seedlings less than among

younger seedlings, ergo tolerances increased (moisture niches expanded) as seedlings aged. Moisture*age was significant for all greenhouse survival metrics and all but one greenhouse performance metrics (Table 3.2). *Triadica* seedling survival increased with age across our greenhouse moisture gradient and under field conditions (Figs. 2 and 4; Tables S1 and S2). The only exception was that seedlings aged 42 and 56 days were less likely to survive and survived for less time (but not significantly less) than seedlings aged 28 days in the greenhouse DRT treatment. We expect this was an experimental artifact from using pots that constrained root depth and architecture of the largest seedlings. Larger plants have greater absolute maintenance requirements and are likely more susceptible to transpirational loss, but typically exhibit greater root depth and area that buffer larger plants against low soil moisture (Parrish and Bazzaz 1985). Thus large seedlings in the greenhouse experiment experienced all costs of their size but not all benefits relative to moisture tolerances.

In the field experiment, the oldest seedlings (62 days) showed the highest net losses in height and leaf count (Table 3.S3) but grew most after initial losses (*personal observation*). This is likely due to flooded and perhaps windy conditions and older seedlings having more biomass to lose as many plants lost tissue or died back but survived. Given *Triadica*'s high capacity for compensatory regrowth (Bruce et al. 1997), shedding tissue when upkeep requirements exceed available resources may be an effective drought tolerance strategy akin to the herbivore tolerance strategy demonstrated by introduced genotypes of *Triadica* (Zou et al. 2008, Huang et al. 2011).

Alternatively, several other mechanisms could act to decouple mature *Triadica* density from average reinvasion pressure. Differences in *Triadica* seed availability

among habitats could promote density-reinvasion decoupling. However, we expect "supersaturated" *Triadica* seed banks subject to self-thinning are commonplace given the high fecundity (Renne et al. 2000) and density of mature *Triadica* where dominant. If so, differences in seed abundance should have relatively little impact on reinvasion because germination and spatial carrying capacity would depend more on abiotic conditions. Notably, this saturation effect would be temporary and diminish as seed banks decrease. Differences in nutrient availability are unlikely to impact germination (Parrish and Bazzaz 1985), but their influence on seedling performance could impact recruitment success in marginal habitats and lead to density-reinvasion decoupling. Ontogenetic changes in nutrient requirements are possible (Parrish and Bazzaz 1985, Quero et al. 2008) and merit study in *Triadica*. Ontogenetic changes in other aspects of *Triadica*'s niche relevant to recruitment or persistence could promote density-reinvasion decoupling if there is variation within and among habitats in the factor(s) associated with these changes. For example, herbivore and disease prevalence vary spatiotemporally, thus ontogenetic increases in herbivore (Barton and Koricheva 2010) or disease resistance or tolerance (Develey-Riviere and Galiana 2007) could lead to density-reinvasion decouplings. However, natural enemies are unlikely to produce such patterns where target exotics are subject to enemy release, as with *Triadica* (Siemann and Rogers 2003b, Siemann et al. 2006).

Differences among source trees may reflect genetic variation among individuals or environmental effects on parent trees (maternal effects). Maternal effects often appear via differences in seed provisioning, which is important to young seedlings. We cannot differentiate between genetic and maternal effects, but our foci are the effects of seedling

age, soil moisture and their interaction. Knowledge of how source trees affect recruitment success is of limited value as it provides little actionable insight into reinvasion.

Implications for restoration and management

Major challenges to restoration of invaded habitats include impacts of exotic management on non-target species and availability of management resources (Rinella et al. 2009, Firn et al. 2010, Kettenring and Adams 2011). Thus exotic management efficiency is vital to restoration efficacy (by minimizing negative impacts on desired species) and resource optimization. Management is most efficient when performed only when necessary and to the degree required, and when selecting sites with the lowest management requirements or highest management benefits (sensu Epanchin-Niell and Hastings 2010). We have established that *Triadica* undergoes ontogenetic moisture niche expansions and it is understood that moisture conditions vary within and among *Triadica*-dominated habitats, thus density-reinvasion decoupling is possible. This has two major implications for restoration and management.

First, mature *Triadica* density is an unreliable predictor of average reinvasion pressure. Unfortunately, publically available management recommendations for *Triadica* and other invasive plants are often based on adult density. Where density-reinvasion decoupling occurs, density-based guidelines can lead to highly inefficient management and/or unnecessary negative non-target impacts (sensu Rinella et al. 2009, Epanchin-Niell and Hastings 2010). Therefore, our foremost recommendation is to base management strategies on niche-based estimates of average reinvasion pressure (detailed in Gabler and Siemann 2012), not on density-based estimates. Reliable estimates based

on *Triadica*'s niche and habitat environmental conditions are less likely to overestimate average reinvasion pressure and typically feasible in its introduced range – particularly now that we better understand *Triadica*'s recruitment niche. Niche-based approaches also enable forecasts of future reinvasion pressure based on short-term weather forecasts, mid-term climate cycles (e.g. ENSO) or long-term climate change projections (sensu Young et al. 2005). Given *Triadica*'s seed longevity (5+ years; Bruce et al. 1997), the latter only applies where external seed input is expected. Reliable niche-based estimates of average reinvasion pressure and forecasts of short-term reinvasion success would greatly benefit restoration planning and cost estimates. This approach should be useful in other systems, especially where invaders exhibit ontogenetic niche expansions. Detailed approaches to estimating reinvasion pressure and specific strategies for various reinvasion scenarios are described in Gabler and Siemann (2012).

Second, habitats with low average reinvasion pressure masked by *Triadica* dominance provide cryptic opportunities for relatively inexpensive and straightforward restorations. Identifying and prioritizing cryptically opportune habitats would enhance restoration efficiency and, given limited resources, could increase extent of successful restoration of *Triadica*-invaded habitats on a landscape scale. This requires estimates of average reinvasion pressure as above, and broader strategies should consider metapopulation dynamics (Buckley et al. 2007, Epanchin-Niell and Hastings 2010). *Triadica*'s selective germination requirements and rapid ontogenetic moisture niche expansion paired with its hydrochorus dispersal and capacity to bank seeds for 5+ years may make it well-equipped to recruit during rare moisture windows. Beyond normal ranges of interannual variation (i.e. 10-year events), extreme weather such as droughts,

floods or tropical cyclones (100-year events) could trigger exceptionally rare but widespread recruitment. Given *Triadica*'s northern Gulf of Mexico distribution, hurricanes in particular could facilitate dispersal and establishment in typically unsuitable habitats. If so, density-reinvasion decouplings and thus cryptically opportune habitats may be quite common.

Managers can exploit *Triadica*'s specific moisture requirements for germination and seedling survival during restoration. Where water control is possible, e.g. in former rice fields, it is likely impractical to maintain flooding to prevent germination due to seed longevity, but one could use flood pulses to kill young seedlings. Efficacy of increasing drainage to reduce moisture to kill seedlings would depend on rainfall and soil. Both approaches would have non-target effects and could substantially influence community development given durations of flooding or drought required to kill seedlings. These tradeoffs should be weighed against management alternatives. Where controlling moisture is not feasible, managers should use knowledge of *Triadica* recruitment requirements and local historical environmental patterns to estimate average reinvasion pressure when developing optimal management strategies. When possible, managers should use local climate forecasts to anticipate short-term recruitment and prepare commensurate management measures if different from base strategy. Actionable changes in *Triadica* reinvasion success need only be predicted in time to perform management while it would have the desired effect. This would be most beneficial in habitats where recruitment is highly pulsed, especially because many *Triadica* management methods are most or only effective when seedlings are young, e.g. burning or grazing. Generally, accurate estimates of average and short-term reinvasion pressure could improve

restoration efficacy, efficiency, and predictability in ecosystem dominated by *Triadica* and other exotic plants, especially those exhibiting ontogenetic niche expansions and subject to density-reinvasion decoupling.

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Table 3.1. Results of repeated measures ANOVA testing effects of soil moisture, source tree, time and their interactions on *Triadica* germination in the germination experiment

factor	d.f.	F_{478}	*p*
moist	5	28.76	**<0.0001**
tree	9	4.18	**<0.0001**
moist*tree	45	1.70	**0.0044**
factor	d.f.	F_{3832}	*p*
time	8	103.28	**<0.0001**
moist*time	40	19.38	**<0.0001**
tree*time	72	3.04	**<0.0001**
moist*tree*time	360	1.42	**<0.0001**
model	539	4.46	**<0.0001**

Table 3.2. Influence of soil moisture, seedling age, source tree and their interactions on *Triadica* seedling survival time (ANODEV χ^2 test), absolute changes (final – initial) in seedling height (ANOVA), leaf count (ANOVA) and stem diameter (square root transformed, ANOVA), and final aboveground biomass ($\log_e$ transformed, ANOVA) in the greenhouse experiment

				absolute change (final – initial)											
	days survived			height			leaf count			stem diameter			final AG biomass		
factor	d.f.	χ^2	*p*	d.f.	F_{221}	*p*	d.f.	F_{221}	*p*	d.f.	F_{210}	*p*	d.f.	F_{218}	*p*
moist	5	102	**<0.0001**	5	38.57	**<0.0001**	5	60.33	**<0.0001**	5	14.37	**<0.0001**	5	21.59	**<0.0001**
age	5	186	**<0.0001**	5	13.80	**<0.0001**	5	10.19	**<0.0001**	5	8.54	**<0.0001**	5	70.43	**<0.0001**
tree	20	37	**0.0190**	20	1.78	**0.0405**	20	1.66	0.06	20	2.27	**0.0069**	20	0.95	0.53
moist*age	25	78	**<0.0001**	24	2.19	**0.0060**	24	1.89	**0.0212**	24	1.23	0.25	24	2.24	**0.0051**
moist*tree	66	183	**<0.0001**	54	0.66	0.94	54	1.07	0.40	52	1.23	0.21	54	1.08	0.37
age*tree	25	52	**0.0012**	20	0.78	0.73	20	1.52	0.10	19	1.31	0.21	20	1.10	0.37
moist*age*tree	42	65	**0.0125**	23	0.95	0.53	23	0.71	0.82	20	1.57	0.09	22	0.95	0.54
model	192	703	**<0.0001**	151	2.80	**<0.0001**	151	3.55	**<0.0001**	145	2.14	**0.0004**	150	4.23	**<0.0001**

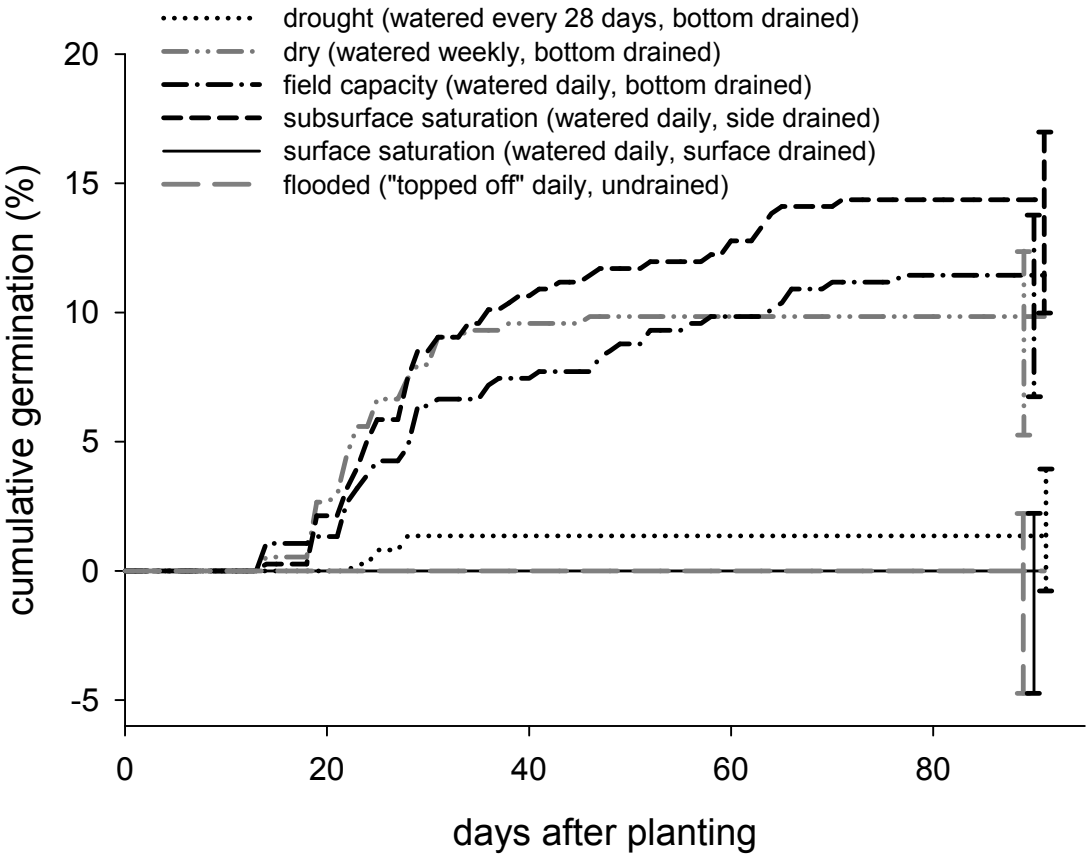

Figure 3.1. Cumulative germination over time by moisture treatment in the germination experiment. Vertical bars at 91 days are 95% confidence intervals for final percent germination.

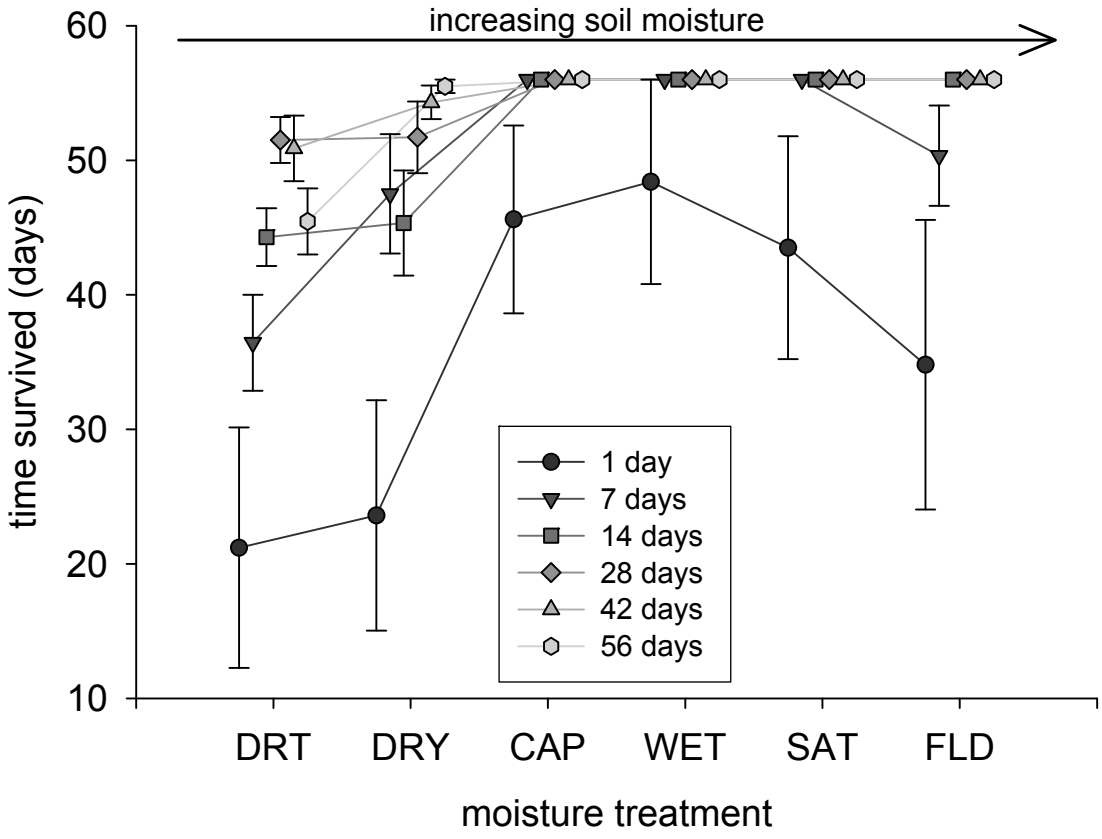

Figure 3.2. Survival time ±1 SE (maximum 56 days) by seedling age (inset legend) and moisture treatment (x axis) in the greenhouse experiment. Ontogenetic niche expansions appear as rapid increases in survival time across the moisture gradient as age increases. Moisture treatments: DRT – well-drained, 25% field capacity; DRY – well-drained, 50% field capacity; CAP – well-drained, well-watered (field capacity); WET – well-watered, subsurface saturation; SAT – well-watered, surface saturation; FLD – constantly flooded.

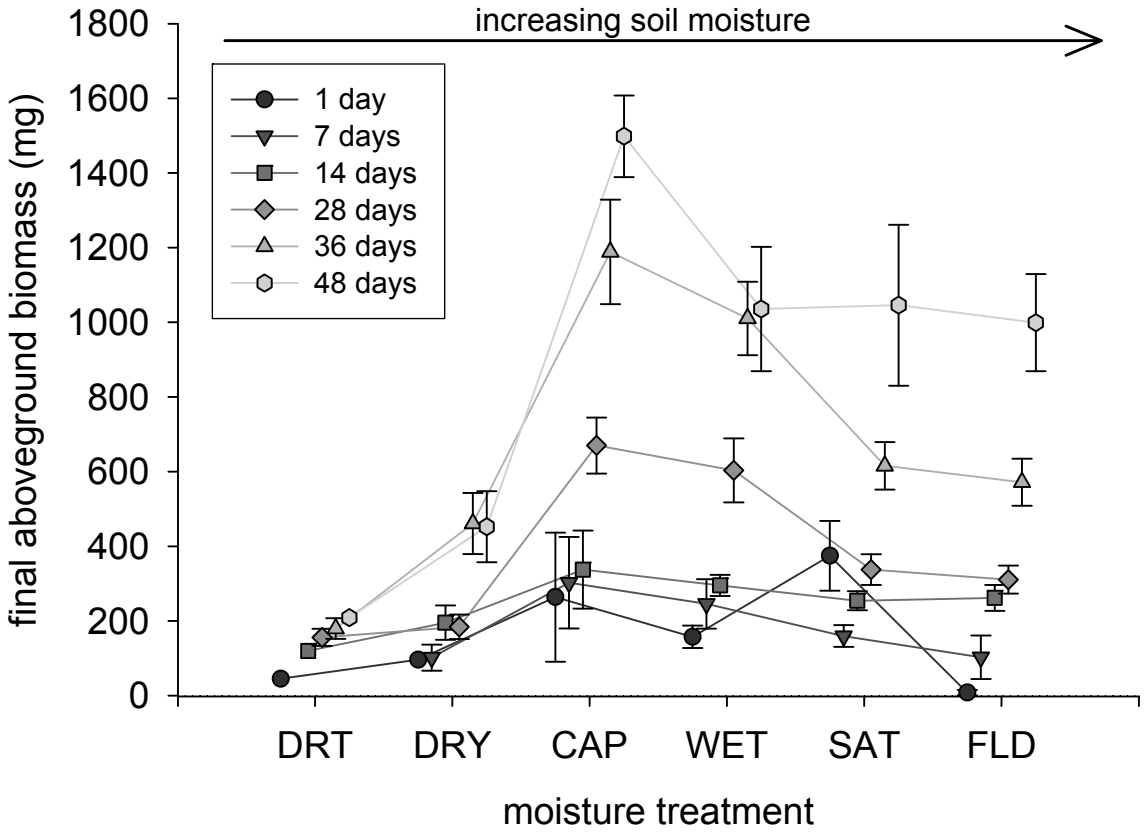

Figure 3.3. Final aboveground biomass ±1 SE by seedling age (inset legend) and moisture treatment (x axis) in the greenhouse experiment. Ontogenetic niche expansions appear as variable increases in mass across the moisture gradient as age increases. Moisture treatments: DRT – well-drained, 25% field capacity; DRY – well-drained, 50% field capacity; CAP – well-drained, well-watered (field capacity); WET – well-watered, subsurface saturation; SAT – well-watered, surface saturation; FLD – constantly flooded.

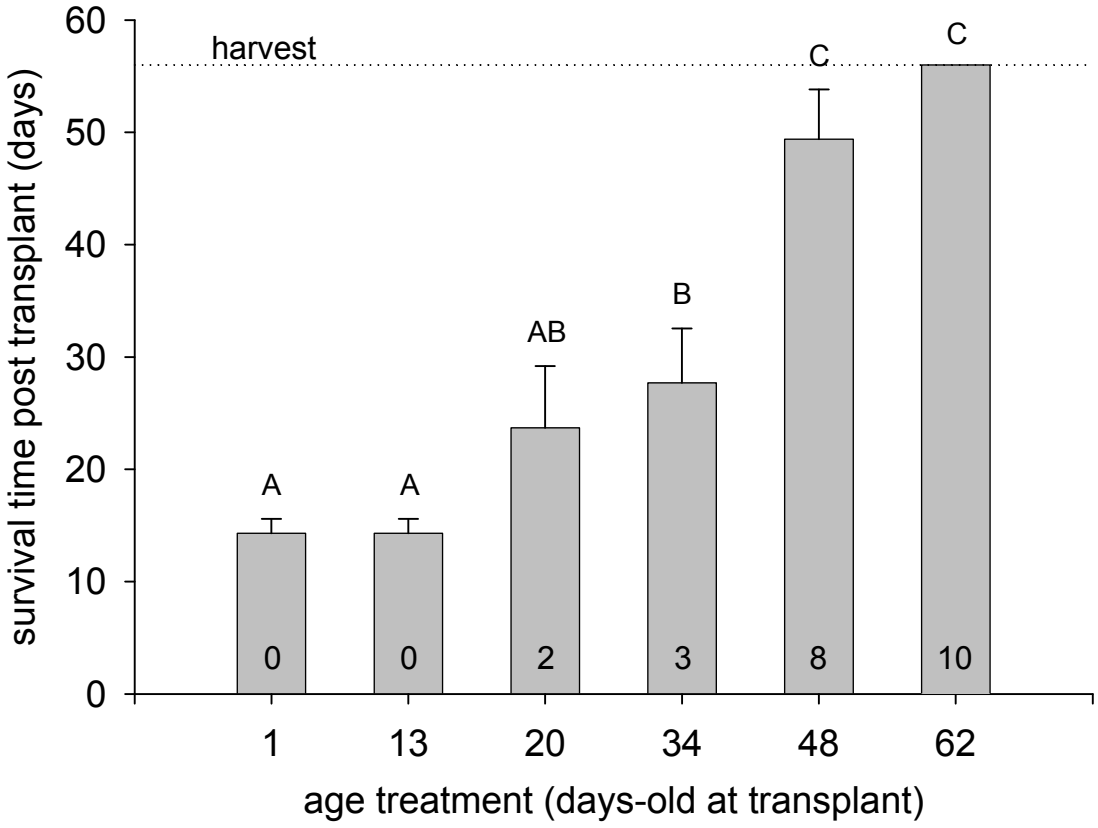

Figure 3.4. Survival time +1 SE of differently aged *Triadica* seedlings in the field experiment. Shared letters above bars indicate means that were not significantly different. Numbers within bars are abundances of live seedlings (maximum ten) after 56 days.

SUPPORTING INFORMATION

Appendix 3.S1. Seed preparation

Appendix 3.S2. Watering protocols

Table 3.S1. Greenhouse survival and performance

Table 3.S2. Field survival and performance

Appendix 3.S1. Seed washing method and rationale

Individual *Triadica* seeds have a waxy outer coat, the thickness and condition of which can influence germination timing (personal observation). Under field conditions, *Triadica* seeds lose their waxy coat rapidly when consumed and defecated by animals or more slowly if not consumed via mold and weathering (Bruce et al. 1997; Renne et al. 2000). To control for this confounding factor, we stripped the waxy coat from all *Triadica* seeds prior to planting. We stirred seeds in batches of ~100 for 2 h in 200 ml water with 20 ml powdered automatic dishwasher detergent. We immediately scrubbed "washed" seeds with a scouring pad over coarse metal screening to strip off any remaining wax, rinsed them in water and dried all seeds thoroughly to avoid cuing germination prior to planting.

References

Bruce, K.A., G.N. Cameron, P.A. Harcombe, and G. Jubinsky. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L) Roxb. Natural Areas Journal **17:**255-260.

Renne, I.J., S.A. Gauthreaux, and C.A. Gresham. 2000. Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) by birds in coastal South Carolina. American Midland Naturalist **144:**202-215.

Appendix 3.S2. Watering protocol for moisture treatments based on field capacity

In the greenhouse experiment, to estimate field capacity in pots and water accordingly we first weighed eight pilot pots at field capacity and after being oven-dried at 75°C for 7 days. Water storage capacity per unit mass varied little but variation in soil mass among pots was significant, so we derived target mass values for pots at 25% and 50% field capacity based on a range of pot masses at 100% field capacity. Prior to initiating DRY or DRT moisture treatments, we weighed each pot, including its seedling, at 100% field capacity using a hanging fish scale and labeled the pot with its target mass value. At every watering we weighed each DRY or DRT pot and added a mass of water equal to the difference between its present and target mass. We added no water if the pot equaled or exceeded the target mass, which was typical near the onset of moisture manipulation. Adjustments to the amount of water added under this protocol to account for seedling biomass were negligible and not performed.

Table 3.S1. *Triadica* seedling survival and performance by moisture and age treatments in the greenhouse experiment. Values transformed for analyses are backward transformed here. Bold values are group maximums and italicized values are group minimums.

soil moisture treatment	seedling age treatment	replicates	survivors	survival (%)	days survived	absolute change (final - initial) height (mm)	leaf count	stem diameter (mm)	final AG biomass (mg)
DRT	1 day	5	1	20	*21.2*	**131**	**4.0**	-0.20	*45*
	7 days	7	0	*0*	36.4	-	-	-	-
	14 days	7	1	14	44.3	25	-2.9	**0.56**	120
	28 days	10	5	**50**	**51.5**	*8*	-3.6	0.11	156
	42 days	8	3	38	50.9	52	-0.7	0.10	180
	56 days	9	1	11	45.4	43	*-8.0*	*-0.20*	**209**
DRY	1 day	5	1	*20*	*23.6*	**142**	**4.1**	*-0.05*	*96*
	7 days	6	3	50	47.5	59	*-1.2*	0.20	102
	14 days	9	3	33	45.3	32	1.8	**1.49**	196
	28 days	10	6	60	51.7	36	-1.0	0.86	184
	42 days	10	8	80	54.3	52	0.4	0.03	**461**
	56 days	10	9	**90**	**55.5**	*26*	-0.7	0.28	452
CAP	1 day	5	3	*60*	*45.6*	113	7.0	*0.02*	*264*
	7 days	6	6	**100**	**56.0**	109	6.6	1.32	303
	14 days	8	8	**100**	**56.0**	*73*	*4.6*	1.33	338
	28 days	10	10	**100**	**56.0**	113	7.4	**2.01**	670
	42 days	8	8	**100**	**56.0**	**196**	**13.1**	1.34	1189
	56 days	10	10	**100**	**56.0**	111	9.6	0.98	**1498**
WET	1 day	5	4	*80*	*48.4*	149	8.9	*0.09*	*158*
	7 days	6	6	**100**	**56.0**	115	6.4	1.26	246
	14 days	9	9	**100**	**56.0**	*88*	*5.4*	1.15	295
	28 days	10	10	**100**	**56.0**	91	7.4	**1.99**	603
	42 days	8	8	**100**	**56.0**	**166**	**11.3**	1.56	1011
	56 days	9	9	**100**	**56.0**	110	9.7	1.53	**1035**
SAT	1 day	6	4	*67*	*43.5*	**148**	**8.4**	*0.95*	375
	7 days	6	6	**100**	**56.0**	63	2.8	1.57	*160*
	14 days	9	9	**100**	**56.0**	*34*	1.7	**1.76**	254
	28 days	10	10	**100**	**56.0**	35	*1.7*	1.63	337
	42 days	10	10	**100**	**56.0**	55	3.7	1.63	616
	56 days	8	8	**100**	**56.0**	50	3.4	0.98	**1046**
FLD	1 day	5	2	*40*	*34.8*	33	*0.0*	*-0.42*	*8*
	7 days	6	4	67	50.3	50	1.4	0.63	103
	14 days	8	8	**100**	**56.0**	47	0.5	**1.66**	262
	28 days	10	10	**100**	**56.0**	*22*	2.2	1.26	311
	42 days	10	10	**100**	**56.0**	**56**	**3.7**	1.30	572
	56 days	9	9	**100**	**56.0**	44	2.1	1.40	**999**
TOTAL		287	222	77	51.6	75	4.3	1.16	539

Table 3.S2. *Triadica* seedling performance by moisture treatment in the greenhouse experiment; 'group' denotes results of post hoc Holm-Bonferroni adjusted pairwise t-tests (treatments sharing the same letter have means that are not significantly different)

	absolute change (final – initial)							
	height (mm)		leaf abundance		stem diameter (mm)		aboveground biomass (mg)	
moisture treatment	mean	group	mean	group	mean	group	mean	group
DRT	35.8	a	-2.5	a	0.09	a	154	a
DRY	42.7	a	-0.1	a	0.40	a	324	a
CAP	119.8	b	8.3	c	1.28	b	814	c
WET	115.2	b	8.1	c	1.37	b	613	bc
SAT	54.9	a	3.1	b	1.47	b	482	ab
FLD	42.1	a	2.0	b	1.24	b	473	ab

Table 3.S3. *Triadica* seedling survival and performance by age treatment in the field experiment

seedling age treatment	replicates	survivors	days survived	absolute change (final - initial) height (mm)	absolute change (final - initial) leaf count	final AG biomass (mg)
1 day	10	0	14.3	-	-	-
13 days	10	0	14.3	-	-	-
20 days	10	2	23.7	51	2.5	1036
34 days	10	3	27.7	104	-5.3	1465
48 days	10	8	49.4	14	-12.4	2506
62 days	10	10	56.0	-59	-19.0	5762
TOTAL	60	23	30.9	-2.7	-13.0	3658

CHAPTER FOUR

Timing of favorable conditions, competition and fertility interact to govern recruitment of invasive Chinese tallow tree in stressful environments

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Timing of favorable conditions, competition and fertility interact to govern recruitment of invasive Chinese tallow tree in stressful environments

ABSTRACT

The rate of new exotic recruitment following removal of adult invaders (reinvasion pressure) influences restoration outcomes and costs but is highly variable and poorly understood. We hypothesize that broad variation in average reinvasion pressure of *Triadica sebifera* (Chinese tallow tree, a major invader) arises from differences among habitats in spatiotemporal availability of realized recruitment windows, which are periods of suitable abiotic conditions long enough to permit exotic establishment given local biotic interactions.

We tested this hypothesis by performing a greenhouse mesocosm experiment that quantified how the duration of favorable moisture conditions prior to flood or drought stress (window duration), competition and nutrient availability influenced *Triadica* success in high stress environments.

Window duration influenced pre-stress seedling abundance and performance and final seedling abundance; it interacted with other factors to affect final performance and biomass, and absolute changes in performance and germination during stress. Stress type and competition impacted final performance and biomass, plus absolute changes in performance, germination and mortality during stress. Final *Triadica* abundance also depended on competition and the interaction of window duration, stress type and competition. Fertilization interacted with other factors to influence final performance and

biomass and absolute change in height during stress, but did not affect *Triadica* abundance or survival.

Overall, longer window durations increased and competition decreased *Triadica* abundance and performance, whereas flood stress (compared to drought) and fertilization increased performance. Interactions among these factors frequently produced different effects in specific contexts.

Results support our 'outgrow the stress' hypothesis and show that temporal availability of favorable abiotic conditions and competition significantly impact *Triadica* recruitment in stressful environments. Stress type was important to recruitment and altered effects of other factors. Our findings enable better niche-based estimates of average and short-term reinvasion pressure, which can improve restoration efficacy and efficiency by informing site selection and optimal management.

INTRODUCTION

Reinvasion pressure, or the rate of new exotic recruitment following removal of mature conspecifics, varies broadly among similarly invaded habitats and is crucial to restoration outcomes and costs but is poorly understood and difficult to predict (Buckley et al. 2007, Kettenring and Adams 2011, Gabler and Siemann 2012). When restoring habitats dominated by an exotic plant, invader density governs strength of impacts on communities and ecosystem functions (Grime 1998) and influences required management methods, which can have diverse impacts on non-target species (Rinella et al. 2009) and vary widely in cost (Epanchin-Niell and Hastings 2010). Accurately estimating reinvasion pressure can improve restoration efficacy and efficiency by informing site selection and optimal management strategies (Gabler and Siemann 2012), but the mechanisms driving its variation are poorly understood despite their importance to restoration and exotic plant control (Kettenring and Adams 2011).

Triadica sebifera (Chinese tallow tree) is a major invader in the southeastern United States that exhibits broad variation in average reinvasion pressure during restorations of habitats it previously dominated (Donahue et al. 2006; Gabler and Siemann, unpublished data). We hypothesize that this variation arises predominantly because differences among invaded habitats in their temporal availability of moisture conditions suitable for *Triadica* recruitment drive differences in average *Triadica* recruitment success (Gabler and Siemann 2012). Differences in average reinvasion pressure can become masked over time by *Triadica* dominance because ontogenetic niche expansions (increases in niche breadth during development) enable *Triadica* to

persist in moisture conditions unsuitable for its recruitment (Chapter Three).

Our ‘outgrow the stress’ hypothesis further posits that short-term reinvasion pressure depends on propagule abundance and spatiotemporal availability of realized recruitment windows, which are akin to ‘safe sites’ (Harper 1977) but emphasize ontogenetic niche expansions (Gabler and Siemann 2012). Realized recruitment windows are periods of variable duration that permit exotics with expanding niches to become established and are determined by abiotic conditions and interspecific interactions with recipient communities. This hypothesis stresses factors that influence seedling growth during temporary periods of suitable environmental conditions and may thus influence establishment success, which Holmgren et al. (2006) demonstrate can influence vegetation structure on a landscape scale and are central to the present work.

Existing hypotheses explaining recruitment or invasion success have long emphasized spatial and/or temporal availability of conditions suitable for germination and establishment. Harper (1977) defined ‘safe sites’ as sites free of specific hazards, e.g. intolerable moisture conditions, and argued that all colonization occurs as a function of their availability. Grubb (1977) described similar ‘regeneration niches’ and Johnstone (1986) elaborated safe sites to consider their dispersion in time. These suggest strict limits in resource availability or climatic tolerances define recruitment opportunities, and indeed many studies demonstrate that temporary variation across distinct abiotic thresholds can permit or preclude plant establishment in stressful habitats (e.g. Balke et al. 2011, Peringer and Rosenthal 2011).

More recent spatiotemporal niche-based invasion hypotheses consider a broader range of biotic and abiotic factors and place greater emphasis on their interactions, e.g.

competition with resident species for fluctuating resources (Davis et al. 2000). Such hypotheses recognize the importance of stochastic disruptions to communities, like earlier theories, but accentuate historical contingencies arising from these and other irregular events, e.g. 'niche opportunity' of Shea and Chesson (2002). They also identify "grayer" abiotic thresholds resulting from stress mediating effects of certain biotic interactions (e.g. Arredondo-Nunez et al. 2009) or life history strategies, e.g. the storage effect (Chesson 2000). Our 'outgrow the stress' hypothesis takes spatiotemporal niche-based invasion hypotheses one step further – albeit strictly in the context of reinvasion – by considering not only fluctuations in the biotic and abiotic environment but also ontogenetic changes in invader environmental tolerances and ultimately the impacts of environment on ontogenetic development of invaders and thus their individual tolerances through time (Gabler and Siemann 2012; Figure 2.2).

Availability of soil resources, including water, and competition for these and other resources are fundamental factors limiting plant distributions (Casper and Jackson 1997, Vitousek et al. 1997), so we expect they are principally important in defining realized recruitment windows. Nutrient availability has been shown to have strong effects on invasion success (Brewer and Cralle 2003, Busey 2003, Tomassen et al. 2004). Fertilization increased *Triadica* invasion pressure in coastal prairies by increasing seedling survival, height and biomass (Siemann et al. 2007), but increased *Triadica* survival in coastal prairies with nutrient addition was not always observed and performance benefits were nutrient specific (Siemann and Rogers 2007).

Water regime is crucial to *Triadica*'s local distribution and can vary considerably on small spatial scales in its introduced range (Bruce et al. 1997). Though established

Triadica seedlings have relatively broad moisture tolerances (Hall and Harcombe 1998, Butterfield et al. 2004), moisture requirements for germination and survival and growth of young seedlings are relatively narrow (Chapter Three). In other systems, interannual variation in precipitation can influence establishment success among years (Bartha et al. 2003) and cause episodic recruitment (Crawley 1990). Preliminary results from experimental restorations of eleven sites dominated by *Triadica* suggest reinvasion pressure correlates with soil moisture, and that addition of native seeds may decrease *Triadica* recruitment success in favorable moisture conditions but, at least early in restoration, increase recruitment success in more stressful conditions (Gabler and Siemann, unpublished data). Interactions between these fundamental factors remain unclear, especially in high stress environments where they may be most important to *Triadica* recruitment success.

We began validating our 'outgrow the stress' hypothesis by demonstrating that *Triadica* undergoes rapid ontogenetic moisture niche expansions, which enable seedlings to tolerate conditions that do not permit germination (i.e. continuous flooding and short-term drought) within two months of germination (Chapter Three). In this work, we continue vetting this hypothesis by investigating realized recruitment windows. Here we quantify how the duration of favorable moisture conditions prior to flood or drought stress (window duration), competition and nutrient availability influence *Triadica* recruitment within highly stressful but variable environments.

Greater understanding of how temporal moisture fluctuations, competition and nutrient availability influence *Triadica* survival and performance would improve estimates of average reinvasion pressure within particular habitats, and would enhance

our ability to predict short-term reinvasion pressure based on climate forecasts (Young et al. 2005, Gabler and Siemann 2012). Knowledge of context-dependent effects of native seed addition or fertilization on *Triadica* recruitment would promote management plans better fit to local circumstances and more able to mitigate or exploit stochastic events such as extreme weather or nutrient or seed pulses. Both provide valuable decision-making tools for restoration and *Triadica* management, and these approaches are applicable in other invaded systems.

We investigated how window duration and key ecological factors influence *Triadica* recruitment in stressful environments by performing a mesocosm experiment manipulating window duration, stress type, competition and fertilization. If availability of realized recruitment windows governs recruitment in stressful habitats, longer window durations prior to stress should increase *Triadica* abundance and performance once stress resumes. If size confers tolerance in plants with ontogenetic niche expansions (Kunstler et al. 2009), factors influencing growth rates should affect recruitment during finite windows of opportunity (Gabler and Siemann 2012), thus fertilization and competition should increase and decrease *Triadica* success, respectively. To better understand how temporal availability of realized recruitment windows influence exotic recruitment and key biotic and abiotic factors shape realized recruitment windows, we ask: (i) How do window duration, competition and fertilization interact to influence *Triadica* seedling abundance and performance? (ii) How does the nature of water stress influence *Triadica* success and/or alter the effects of other factors?

METHODS

Focal species

Chinese tallow tree [*Triadica sebifera* (L.) Small, Euphorbiaceae; synonym *Sapium sebiferum;* '*Triadica*' throughout] is a major invasive species in the southeastern United States naturalized from Texas to Arkansas and eastward from Florida to North Carolina and in California (Bruce et al. 1997, Aslan 2011). *Triadica* aggressively displaces native plants in grasslands (e.g. imperiled coastal prairies), wetlands and forests and can form monocultures in only two decades (Bruce et al. 1997, Harcombe et al. 1999). *Triadica* is a superior competitor due to a combination of high growth rates (Lin et al. 2004), prolific seed production (Renne et al. 2000), broad abiotic tolerances (Jones and McLeod 1989, Butterfield et al. 2004) and low herbivore loads in its introduced range (Siemann and Rogers 2003).

Triadica seeds exhibit dormancy and can remain viable in seed banks for 5+ years (Bruce et al. 1997). Seeds require specific abiotic conditions to cue germination, namely widely oscillating day-night temperatures, which are characteristic of exposed soil and promote *Triadica* germination in disturbed conditions (Nijjer et al. 2002, Donahue et al. 2004, 2006), and moist but unsaturated soils, which promote germination in moisture conditions optimal for seedling survival and growth (Chapter Three). Established *Triadica* juveniles have broad moisture tolerances (Hall and Harcombe 1998, Butterfield et al. 2004), but the moisture requirements of newly germinated *Triadica* seedlings are relatively narrow and rapidly broaden in the first months of development to enable persistence in conditions ranging from constant flooding to short-term drought (an ontogenetic moisture niche expansion); survival in flooded conditions depends strongly on plant size, specifically whether seedlings have any emergent leaves (Chapter Three).

We expect rapid moisture niche expansions early in ontogeny are crucial to *Triadica* establishment success during brief windows of favorable conditions in temporally variable environments. Furthermore, we hypothesize that size confers moisture tolerance and thus factors such as competition and nutrient availability also influence minimum establishment time and recruitment success during abiotic windows of opportunity (Gabler and Siemann 2012).

Greenhouse mesocosm experiment

We manipulated duration of favorable moisture conditions prior to water stress (window duration), competition and nutrient availability in mesocosms and quantified *Triadica* abundance, survival and performance through a period of water stress. Our balanced full factorial design used 2.8 L pots with five window duration, two competition, two fertilization and two stress type treatments with 10 replicates per treatment combination (n = 400 pots). In July 2008 we filled 2.8 L tapered square plastic Treepots (36 cm tall, 6-10 cm diameter; Stuewe & Sons, Oregon, USA) with ~2 L field soil collected from Justin Hurst Wildlife Management Area (JHWMA) in southeast Texas and randomly assigned treatments to each. Soils collected near 28.959502 N, -95.461348 W were expansive Pledger (85%) and Brazoria Clay (10%) vertisols (very-fine, smectitic, hyperthermic Typic Hapluderts) with 60-80% clay content. JHWMA is limited-access public land owned and managed by the Texas Parks and Wildlife Department, whose staff granted us access and permission to collect soil. We added 10 washed *Triadica* seeds to each pot from a well-mixed batch collected in 2007 from source trees in southeast Texas. This provided relatively dense seed banks (~1000

seeds/m^2) typical of habitats dominated by *Triadica*. We housed pots in a climate controlled greenhouse under natural light with day temperatures of 29-31°C and night temperatures of 19-21°C, which approximates spring in southeast Texas. See Chapter Three for additional site description and seed preparation protocols.

We established five window duration treatments by exposing pots to identical well-drained and well-watered conditions for 4, 6, 8, 10 or 12 weeks before imposing water stress. We established two competition treatments by adding nothing (control, CON) or 0.5 g each of *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Leersia oryzoides* (L.) Sw. (rice cutgrass) seeds at the time of *Triadica* seed addition (competition, COMP). We chose these species to ensure that natives were present and alive to compete with *Triadica* in both types of water stress. Both have relatively broad moisture tolerances, but *Schizachyrium* tolerates substantial drought whereas *Leersia* tolerates persistent flooding. We established two fertilization treatments by adding water (control, CON) or 4 g/m^2 nitrogen, 1.3 g/m^2 phosphorus, 2.7 g/m^2 potassium and micronutrients (Ultra Turf fertilizer; Vigoro Corp., Illinois, USA) dissolved/suspended in water at seed addition and 8 weeks later (fertilized, FERT). We established treatments for type of water stress by either blocking drainage and "topping off" pots at watering so 8-10 cm of standing water persisted (flood, FLD) or discontinuing watering altogether (drought, DRT) after the designated period of favorable conditions ended. We watered according to treatments and weeded pots not subject to competition thrice weekly. In each pot we quantified *Triadica* abundance, height and leaf count of individual *Triadica* seedlings, and percent cover (visual estimate) and maximum height of native plants at the onset of water stress and 14 and 28 days later. After final surveys we harvested living

aboveground biomass of all *Triadica* seedlings from all treatments, native plants from competition treatments, and root biomass of living *Triadica* seedlings from 12-week window treatments. Biomass samples were oven-dried at 70°C for 48 h and weighed.

To evaluate effects of experimental treatments on *Triadica* abundance, we fit abundance (count) data using generalized linear models (GLM's; 'glm' in R 2.13; R Foundation for Statistical Computing, Vienna, Austria) with Poisson probability distributions. We used analysis of deviance (ANODEV, a form of likelihood ratio testing; 'anova' in R) with chi-square tests to determine whether window duration, competition, fertilization, stress type and/or their interactions influenced pre-stress and final seedling abundance, and number of germinants and deaths during stress. For deaths we excluded pots without *Triadica* seedlings. To examine effects of experimental treatments on *Triadica* performance, we fit performance data with GLM's using a maximum likelihood approach to parameter estimation ('glm' in R) because variation among treatments in number of pots with *Triadica* seedlings produced unbalanced sample sizes (Bolker et al. 2009). We then used ANOVA ('aov' in R) to test whether treatments and/or their interactions influenced pre-stress and final pot sums of seedling heights and leaf abundances; sums of stem, leaf, root, aboveground and total biomasses; absolute changes (final – initial) in seedling heights and leaf abundances; and root:shoot. Response variables incorporating root biomass include the 12 week window treatment only and were $\log_e$ transformed, absolute changes were untransformed and all other *Triadica* performance metrics were square root transformed for analyses. For pots with native competition, we also fit GLM's and used ANOVAs to evaluate treatment effects on native plants in terms of their pre-stress and final percent cover (arcsine transformed) and

maximum height (untransformed), final aboveground biomass (square root transformed) and absolute changes in cover and maximum height (untransformed). Lastly, we used repeated measures ANOVAs ('aov' in R) to test effects of window duration, competition, fertilization, stress type, time and their interactions on *Triadica* seedling abundance, sums of *Triadica* seedling heights and leaf abundances, and native plant cover and maximum height. Error was partitioned across subjects (pots) for factors excluding time and within subjects for factors including time. We used Holm-Bonferroni adjusted pairwise t-tests to identify differences between treatment means. We used pot sums instead of averages because we are more interested in population level effects and because averages are confounded by uncontrolled variation in *Triadica* seedling ages.

RESULTS

Triadica abundance

Pre-stress *Triadica* abundance depended solely on window duration, but window duration, competition and the win*stress*comp interaction influenced final *Triadica* abundance (Table 4.1; Figure 4.1a-b). Pre-stress and final seedling abundances increased with window duration, and final *Triadica* abundances in 8 and 12 weeks treatments were significantly higher (2.2-fold greater) than in the 4 weeks treatment ($P = 0.026$ and 0.018, respectively; $P = 0.051$ for 10 versus 4 weeks treatments). Stress type and competition affected abundances of germinants and deaths (Table 4.1; Figs. 1c, d). Germinants and deaths were rare during flood stress and ~10-fold more frequent during drought stress. Competition increased number of deaths 75% and reduced final seedling abundance 46%

and germinant count 65%. However, native competition increased germinant abundance in the 4 weeks window treatment (win*comp interaction, $P = 0.0052$; Figure 4.1c) and particularly during drought stress, which produced the atypical final seedling abundance patterns observed among 4 weeks treatments (win*stress*comp interaction, $P = 0.0018$; Figure 4.1b). Repeated measures of *Triadica* abundance also depended on window duration, competition and comp*time and stress*comp*time interactions (Figure 4.1e; see Table 4.S1 in Supporting Information). *Triadica* abundances over time demonstrated stability during flood stress, early increases during drought stress without competition, and late decreases during drought stress with competition (Fig 1e), which underlie both aforementioned interactions.

Triadica performance

Pre-stress sums of *Triadica* seedling heights and leaf abundances (totals per pot) depended only on window duration (Table 4.2; Figure 4.2a-b). Final sums of heights and leaves and pot totals of stem, leaf, and aboveground biomasses were independent of the main effect of window duration, but all depended on one or more interactions that included window duration (Table 4.2). Post-stress *Triadica* performance generally increased with window duration; pots given >8 weeks of favorable conditions had 62% more seedling height, 24% more leaves, and 2.3- to 2.7-fold more aboveground biomass than pots given 4 weeks. Stress type and competition affected all final performance metrics (Table 4.2; Figs. 2c-d and 3a-d). Overall, flooded pots exhibited 46% more seedling height, twice the leaf abundance, 2.8-fold more stem biomass, 3.5-fold more leaf biomass and 3.1-fold more aboveground biomass compared to pots subject to drought

stress. Pots with native competitors produced 16% less *Triadica* height, 26% fewer leaves, and 33-36% less aboveground biomass than pots without native plants. Fertilization had insignificant main effects but interacted with other factors to influence all final performance metrics (Table 4.2). Fertilization increased aboveground biomass 23-31% overall. Among 12 week window treatments, stress type influenced sums of root (2.5-fold higher in flood; $F_{1,23} = 5.2$, $P = 0.0364$) and whole plant biomass (2.8-fold higher in flood; $F_{1,23} = 6.3$, $P = 0.0231$), and root:shoot (ratio of sums) depended on competition (2.4-fold higher with competition; $F_{1,23} = 7.2$, $P = 0.0165$).

Interactions among treatments were crucial to *Triadica* performance. All final performance metrics depended on win*stress*fert (Table 4.2). Fertilization tended to increase *Triadica* performance in flood stress and decrease or not affect performance in drought stress (stress*fert), but not consistently across window duration treatments (win*stress*fert; Figs. 2c-d and 3a-d). Stem, leaf and aboveground biomasses depended on win*comp because competition had stronger negative effects among longer window durations, stress*fert (above), and comp*fert because fertilization increased *Triadica* biomass without competition but decreased biomass with competition (Figs. 3a-d). The win*stress interaction influenced final leaf abundance and leaf biomass because differences between flood and drought treatments were larger among longer windows (Figs. 2d and 3b). Leaf biomass also depended on stress*comp because competition had stronger relative negative effects among flood treatments than drought, and stress*comp*fert because competition reduced leaf biomass in drought but not flood without fertilization and reduced leaf biomass in flood but not drought with fertilization (Figure 4.3b). Stem biomass depended on win*stress*comp*fert because (i) under

drought stress, biomass increased as window duration increased with no competition and no fertilization (CON, CON) but decreased as windows increased with competition and fertilization (COMP, FERT; Figure 4.3c); whereas (ii) under flood stress, biomass increased as windows increased with no competition and fertilization (CON, FERT) but decreased as windows increased with competition and no fertilization (COMP, CON), and zero seedlings survived in 4 weeks window treatments with competition (Figure 4.3d).

Repeated measures of sums of *Triadica* heights and leaves depended on window duration, stress, time and stress*time, competition*time and stress*comp*time interactions (Figure 4.2e-f; see Table 4.S1). Competition, win*time and win*stress*fert also influenced sums of leaves (Figure 4.2f), and win*stress*comp*time also affected sum of heights (Figure 4.2e; see Table 4.S1). *Triadica* heights and leaves generally increased during flood stress (more without competition), increased early during drought without competition (as above), and decreased late during drought with and, for leaf sums only, without competition (Figure 4.2e-f). These patterns drove the W*S*C*T interaction given that performance also changes with window duration as described above.

Absolute changes during stress in sums of *Triadica* heights and leaves depended on stress type, competition and stress*comp (see Table 4.S2; Figure 4.S1a-c). Window duration also influenced changes in leaf abundance, and stress*fert and W*S*C*F also affected changes in heights. Unlike the prior stress*comp effect, the decrease in change with competition was stronger during drought stress than flood, and was the only negative change. The stress*fert interaction arose because fertilization decreased changes in height during flood stress and increased them during drought. Here, W*S*C*F

influenced changes in height because (i) under drought stress, increases in height were reduced as windows increased without competition, but increases in height became decreases as windows increased with competition (see Figure 4.S1a); however, (ii) under flood stress, increases in height enlarged as windows increased with neither competition nor fertilization (CON, CON) but increases in height shrank as windows increased with competition or no competition plus fertilization (see Figure 4.S1b).

Native plant abundance and performance

Native plants were only present in competition pots, so competition does not apply. Pre-stress native plant percent cover and maximum height depended solely on window duration (see Table 4.S3; Figure 4.S2a-b). Window duration and win*stress influenced final percent cover and maximum height, aboveground biomass, and absolute changes in cover and maximum height (see Table 4.S3). As window duration increased, final height and biomass typically increased, but final cover and changes in cover generally decreased; changes in height were lowest in intermediate windows (see Figs. S1d-e and S2c-d, g). Stress type also affected final cover, biomass and change in cover, and win*stress*fert impacted final cover (see Table 4.S3). Native abundance and performance were typically lower in drought treatments than flood, but this difference was inconsistent among window duration treatments and sometimes reversed (win*stress). Fertilization effects on final cover were also inconsistent across window and stress treatments (win*stress*fert; see Figure 4.S2c). Repeated measures of native cover and maximum height depended on time, win*time, stress*time and win*stress*time (see Table 4.S4). Stress and win*stress also affected cover and window duration further

influenced maximum height. Cover generally decreased over time but shorter window treatments increased during flood (win*stress*time); maximum height typically increased during stress (see Figure 4.S2e-f).

DISCUSSION

Reinvasion pressure is vital to restoration outcomes and costs, but it can vary widely among equivalently invaded habitats and is difficult to predict (Buckley et al. 2007, Kettenring and Adams 2011, Gabler and Siemann 2012). Niche-based invasion models can be used to develop estimates of reinvasion pressure. Current niche-based invasion hypotheses (e.g Davis et al. 2000, Shea and Chesson 2002) emphasize spatiotemporal variability in abiotic and biotic conditions but do not consider effects of ontogenetic niche shifts (ONSs) in environmental tolerances of invaders. It is unknown how common ONSs are among invaders, as niche shifts in plants are understudied in general (Quero et al. 2008), but ONSs can have profound impacts on plant species distributions and population dynamics (Parrish and Bazzaz 1985, Eriksson 2002, Donohue et al. 2010), plant-plant interactions (Miriti 2006, Quero et al. 2008) and succession (Young et al. 2005).

We know the problematic invader *Triadica sebifera* (Chinese tallow tree) exhibits rapid ontogenetic niche expansions (one type of ONS) in its moisture tolerance early in life, and that this is a probable factor in its broad variation in average reinvasion pressure among restorations of *Triadica*-dominated ecosystems (Donahue et al. 2006; Chapter Three). In cases involving invaders with expanding abiotic niches like *Triadica*, our

'outgrow the stress' hypothesis (Gabler and Siemann 2012) holds that exotic establishment success and thus reinvasion pressure are determined by spatiotemporal availability of realized recruitment windows when exotic propagules are abundant (which is typical in exotic-dominated habitats). This study tested basic tenants of this hypothesis, namely that there is a minimum establishment time for exotics wherein they must germinate and grow to a stage or size capable of tolerating subsequent conditions, and that factors influencing growth can influence individual attainment of required tolerances and thus permit or preclude recruitment. Our results were not this black and white, but they clearly validate the following core predictions of the 'outgrow the stress' hypothesis:

Prediction 1 – Recruitment success will scale with temporal availability of abiotic windows. Our results clearly show that longer periods of favorable conditions prior to water stress (availability of abiotic windows) increased *Triadica* abundance before and after subsequent stress periods. The benefit of longer window durations to final *Triadica* performance was strong overall but less straightforward due to inconsistent or no changes, and even decreases, in certain performance response variables within particular treatment contexts. This significantly increased variance among window duration treatments and likely led to the insignificant main effects of window on performance metrics. Perhaps due to the dearth of studies considering ontogenetic niche expansions, to our knowledge there are no other direct experimental tests of whether longer abiotic windows increase recruitment in stressful environments. However, observational studies often link longer periods between stressful events to increased recruitment; for example, Stokes (2008) observed enhanced *Salix nigra* recruitment and relative growth rates in

areas subject to less frequent inundation. Manipulation of abiotic window duration in the field poses significant logistical challenges, but is necessary to experimentally test this prediction in a more natural setting. Notably, window frequency is another aspect of window availability that should affect average reinvasion pressure in ways window duration does not and merits investigation.

Final performance only decreased with window duration in terms of stem biomass and under either drought stress with competition and fertilization or flood stress with competition and no fertilization, i.e. as part of a complex four-way interaction. We expect the mechanism here simply reflects different limiting resources and levels of demand. Under drought stress, water is most limiting and competition plus fertilization basically created both the highest individual demands and strongest competition for water. Fertilization exacerbated water limitation by increasing the size of native plants and *Triadica* seedlings (which were greatest after the longest windows of favorable conditions) and thus produced the highest total water demand amidst the strongest inter- and intraspecific competition for water. Under flood stress with competition, *Triadica* was likely most limited by light availability followed by soil nutrients, but native height was independent of fertilization, so having competition and no fertilization reduced both light availability and *Triadica*'s capacity to capture it. We observed a similar decrease in success among the largest plants in the driest moisture treatments when investigating *Triadica*'s moisture niche expansions (Chapter Three). Notably, in that study we also observed the highest flood-induced mortality among *Triadica* seedlings whose heights were shorter than sustained flood depth, which explains observed mortality and final seedling abundances of zero in flood treatments with window durations of 4 weeks – our

only apparent case of a “hard” minimum establishment time.

Prediction 2 – Environmental factors affecting growth will influence recruitment in the same manner during finite windows of opportunity. Our results clearly show that competition with native plants generally decreased *Triadica* performance and had an associated negative effect on *Triadica* seedling abundance. Fertilization increased *Triadica* performance overall, particularly biomass, but had no associated effect on abundance. Stress type resulted in differences in final performance metrics between pots exposed to flood versus drought that were generally larger than differences between competition treatments, but stress type only affected *Triadica* abundance in interaction with window duration and competition.

If size confers tolerance (Kunstler et al. 2009), factors that increase (e.g. fertilization) or decrease growth rates (e.g. competition) should have similarly positive or negative effects on recruitment of plants with expanding niches in stressful environments. Thus our findings could be considered partial support for this aspect of the ‘outgrow the stress’ hypothesis. However, the hypothesis states that changes in growth rate affect recruitment success by altering minimum establishment times and acknowledges that differences in time required for establishment do not mandate differences in recruitment in all cases. Rather, recruitment ultimately depends on whether minimum establishment times exceed the duration of favorable conditions available in a particular habitat. Only when environmental factors increase establishment time to a length exceeding duration of suitable conditions or decrease it to a duration less than or equal to available windows should they act to influence abundance of recruits. Furthermore, performance is a meaningful aspect of recruitment success and reinvasion pressure in its own right, and it

may affect future survival in manifold ways. Therefore, it would be an overstatement to conclude that factors are not having an effect on recruitment unless they affect abundance.

Implications for restoration and management

We have quantified realistic baselines for temporal durations of suitable environmental conditions required for *Triadica* establishment (i.e. realized recruitment windows) that are consistent with both its known patterns of ontogenetic niche expansions (Chapter Three) and observed restoration outcomes in habitats it dominated (Donahue et al. 2006; Gabler and Siemann, unpublished data). Further, we have quantified how certain key factors, which are relatively controllable by managers during restoration, may independently alter or interact to influence establishment times and *Triadica* seedling abundance and performance within particular recruitment windows. These results are directly pertinent to our understanding of *Triadica*'s reinvasion mechanisms and can immediately contribute to improving estimates of average reinvasion pressure within specific habitats based on historical or edaphic conditions, and these results may particularly enhance our ability to predict short-term reinvasion pressure based on climate forecasts (Young et al. 2005, Gabler and Siemann 2012).

Additionally, our identification of important interactions among the nature of water stress, competition and nutrient availability provide valuable data on how specific context-dependent effects of native seed addition or fertilization are likely to influence management results. For example, the use of fertilizer in combination with native seed addition in low water environments could provide an unexpected opportunity and

additional capacity to reduce *Triadica* success with specialized management. Similar non-intuitive, context-specific exotic management methods have been identified in other systems as well. For example, Firn et al. (2010) found that adding fertilizer to California grasslands and permitting introduced ungulate grazers to remain on site increased palatability and herbivory of invasive *Eragrostis curvula*, and ultimately led to greater reductions in *Eragrostis*, lower novel invasion by an exotic forb and plant communities more similar to historic targets than did commonly accepted methods of herbicide application and removal of introduced grazers. Identification of specialized control methods encourages *Triadica* management plans better fit to local circumstances and more able to mitigate or exploit stochastic events such as extreme weather or nutrient or seed pulses. The reinvasion pressure framework further validated by this work is a valuable tool that can be used to optimize site selection and exotic management strategies during restoration or invasive plant control, especially where exotics exhibit ontogenetic niche expansions.

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Table 4.1. Results of ANODEVs testing effects of experimental treatments on *Triadica* abundance. Experimental treatments include window duration (W), stress type (S), competition (C), fertilization (F) and their interactions. Pre-stress and final abundances are the numbers of live *Triadica* seedlings observed before and after 28 days of water stress, respectively. Germinants and deaths during stress are abundances of those instances observed during this stress period.

		pre-stress abundance		final abundance		germinants during stress			deaths during stress	
factor	d.f.	χ^2	*p*	χ^2	*p*	χ^2	*p*	d.f.	χ^2	*p*
Window	4	15.7	**0.0035**	10.4	**0.0349**	2.7	0.61	4	0.5	0.97
Stress	1	2.0	0.15	1.0	0.31	18.6	**<0.0001**	1	16.2	**<0.0001**
Comp	1	1.5	0.22	9.4	**0.0021**	6.5	**0.0106**	1	5.7	**0.0165**
Fert	1	0.7	0.39	1.4	0.23	0.3	0.56	1	0.0	0.85
W*S	4	4.7	0.32	7.2	0.13	2.6	0.63	4	6.0	0.20
W*C	4	0.3	0.99	1.6	0.81	14.8	**0.0052**	4	1.2	0.87
S*C	1	0.5	0.46	2.8	0.09	0.0	0.84	1	2.6	0.11
W*F	4	1.3	0.87	2.5	0.64	4.0	0.41	4	0.6	0.96
S*F	1	0.0	0.86	0.4	0.54	0.4	0.55	1	1.9	0.17
C*F	1	0.9	0.34	0.0	0.92	0.1	0.71	1	0.0	0.88
W*S*C	4	9.1	0.06	17.2	**0.0018**	3.9	0.42	3	0.0	1.00
W*S*F	4	6.6	0.16	4.9	0.30	2.0	0.73	4	0.0	1.00
W*C*F	4	3.9	0.42	2.0	0.73	1.6	0.80	4	4.4	0.35
S*C*F	1	1.0	0.33	0.0	0.92	0.0	1.00	1	0.0	1.00
W*S*C*F	4	1.8	0.76	2.7	0.60	0.0	1.00	2	0.0	1.00

Table 4.2. Results of ANOVAs testing effects of experimental treatments on *Triadica* performance. Experimental treatments include window duration (W), stress type (S), competition (C), fertilization (F) and their interactions. Pre-stress and final sums of heights and leaves are summed totals within individual mesocosm pots of *Triadica* seedling heights and leaf abundances observed before and after 28 days of water stress, respectively. Stem, leaf and aboveground biomasses are sums of dry tissue masses collected from individual pots after 28 days of water stress. All values were square root transformed for analyses.

		pre-stress sum of heights		pre-stress sum of leaves			final sum of heights		final sum of leaves		stem biomass		leaf biomass		aboveground biomass	
factor	d.f.	F_{91}	*p*	F_{91}	*p*	d.f.	F_{94}	*p*	F_{94}	*p*	F_{94}	*p*	F_{94}	*p*	F_{94}	*p*
Window	4	3.7	**0.0100**	3.9	**0.0076**	4	2.0	0.11	0.8	0.51	1.9	0.13	1.4	0.24	1.5	0.21
Stress	1	3.9	0.05	3.0	0.09	1	14.4	**0.0003**	53.3	**<0.0001**	33.2	**<0.0001**	42.7	**<0.0001**	42.6	**<0.0001**
Comp	1	0.1	0.77	1.3	0.26	1	4.6	**0.0355**	17.0	**0.0001**	9.2	**0.0035**	10.6	**0.0018**	11.0	**0.0016**
Fert	1	1.2	0.27	0.1	0.70	1	0.7	0.39	0.5	0.49	3.8	0.06	2.9	0.10	3.3	0.07
W*S	4	0.2	0.94	0.3	0.85	4	0.3	0.84	3.1	**0.0231**	1.9	0.13	2.8	**0.0357**	2.0	0.11
W*C	4	0.6	0.66	1.1	0.36	4	1.7	0.17	1.7	0.15	3.0	**0.0246**	4.4	**0.0037**	3.7	**0.0090**
S*C	1	0.4	0.53	1.7	0.20	1	1.0	0.32	1.0	0.33	3.6	0.06	7.7	**0.0074**	4.0	0.05
W*F	4	1.1	0.37	1.1	0.35	4	2.5	0.05	1.9	0.12	2.1	0.10	2.0	0.10	2.0	0.11
S*F	1	0.1	0.80	0.1	0.75	1	0.1	0.76	0.1	0.75	4.1	**0.0474**	8.8	**0.0044**	5.6	**0.0213**
C*F	1	0.8	0.38	1.9	0.17	1	0.2	0.70	0.5	0.48	8.9	**0.0041**	8.8	**0.0044**	7.9	**0.0067**
W*S*C	3	0.3	0.80	0.4	0.73	2	0.6	0.57	2.2	0.12	1.3	0.28	3.1	0.05	1.3	0.27
W*S*F	4	0.7	0.58	0.6	0.65	4	2.5	**0.0485**	3.7	**0.0087**	3.5	**0.0132**	4.2	**0.0048**	3.3	**0.0162**
W*C*F	3	0.3	0.81	0.2	0.88	4	0.5	0.75	2.2	0.08	0.3	0.88	1.1	0.38	0.4	0.79
S*C*F	1	0.4	0.51	0.0	0.93	1	0.2	0.63	1.0	0.32	1.4	0.25	4.3	**0.0422**	1.2	0.27
W*S*C*F	2	1.1	0.35	1.6	0.22	1	2.1	0.15	0.0	0.91	4.7	**0.0336**	3.4	0.07	3.2	0.08

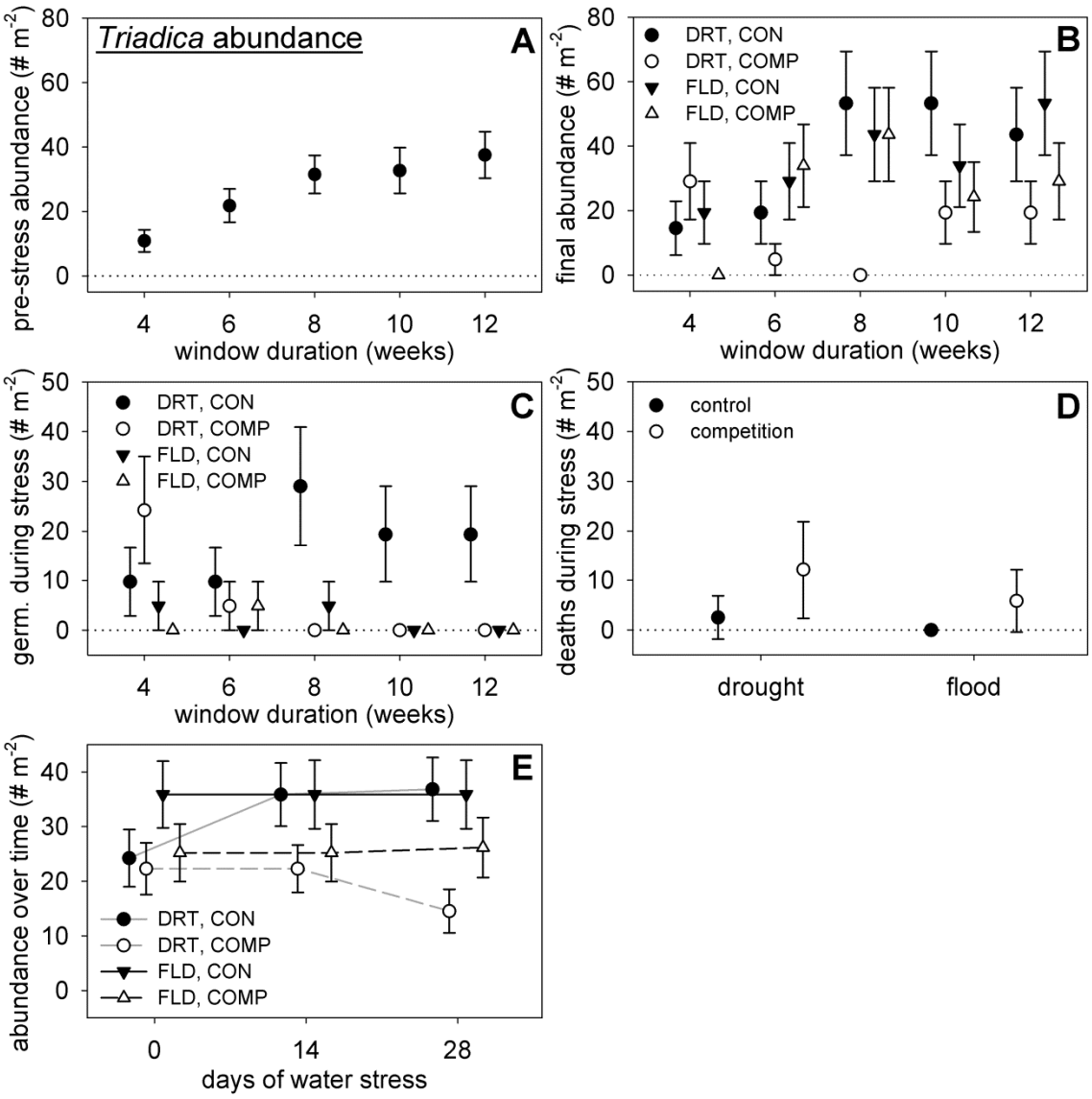

Figure 4.1. Effects of experimental treatments on five metrics of *Triadica* abundance. Each panel represents one abundance metric (means ±1 SE) broken down by treatments that significantly affected that metric. Legend: stress type – drought (DRT) or flood (FLD); competition – natives added (COMP) or control (CON). A – Pre-stress *Triadica* abundance was higher in longer window duration treatments. B – Final abundance was higher with longer window durations and generally lower with drought stress or competition. C – Flood or competition generally reduced germination during

stress; more germinants were observed after shorter windows but only with competition. D – More seedlings died during stress when subject to drought or competition. E – *Triadica* abundance over time was steady under flood stress but increased early without competition and decreased later with competition under drought stress.

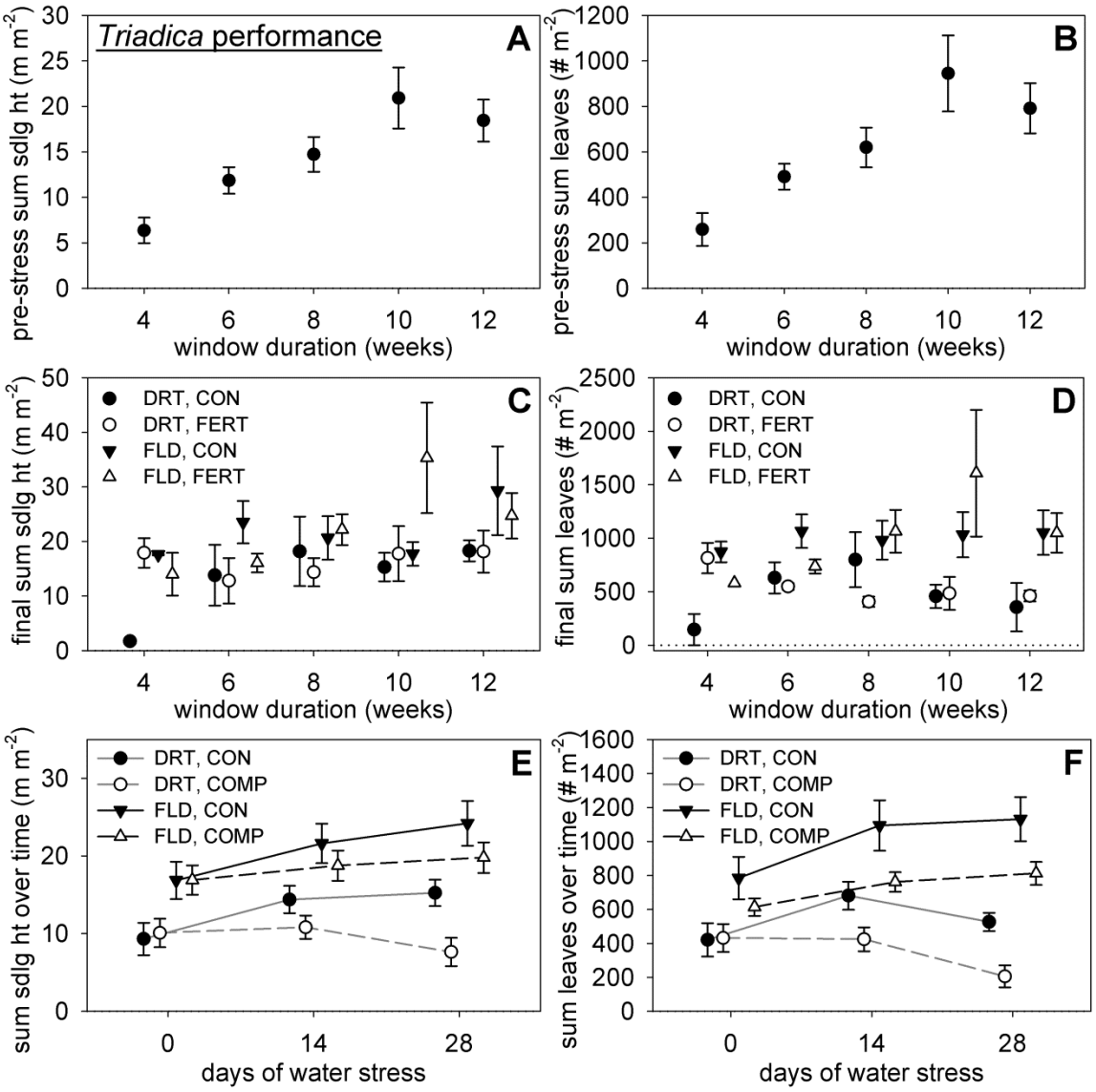

Figure 4.2. Effects of experimental treatments on six metrics of *Triadica* performance. Each panel represents one performance metric (means ±1 SE) broken down by treatments that significantly affected that metric. Legend: stress type – drought (DRT) or flood (FLD); competition – natives added (COMP) or control (CON); fertilization – NPK added (FERT) or control (CON). Pre-stress pot sums of *Triadica* seedling heights (A) and leaf abundances (B) were higher in longer window duration treatments. Final pot sums of seedling heights (C) and leaves (D) were generally greater

with longer window durations, lower with drought or competition, and higher with fertilization but only in flood treatments. Sums of *Triadica* seedling heights (E) and leaves over time (F) most often increased, but leaves initially increased and later decreased under drought conditions without competition, while heights and leaves later decreased under drought with competition. Differences between stress types after 0 days of stress in E and F are not significant.

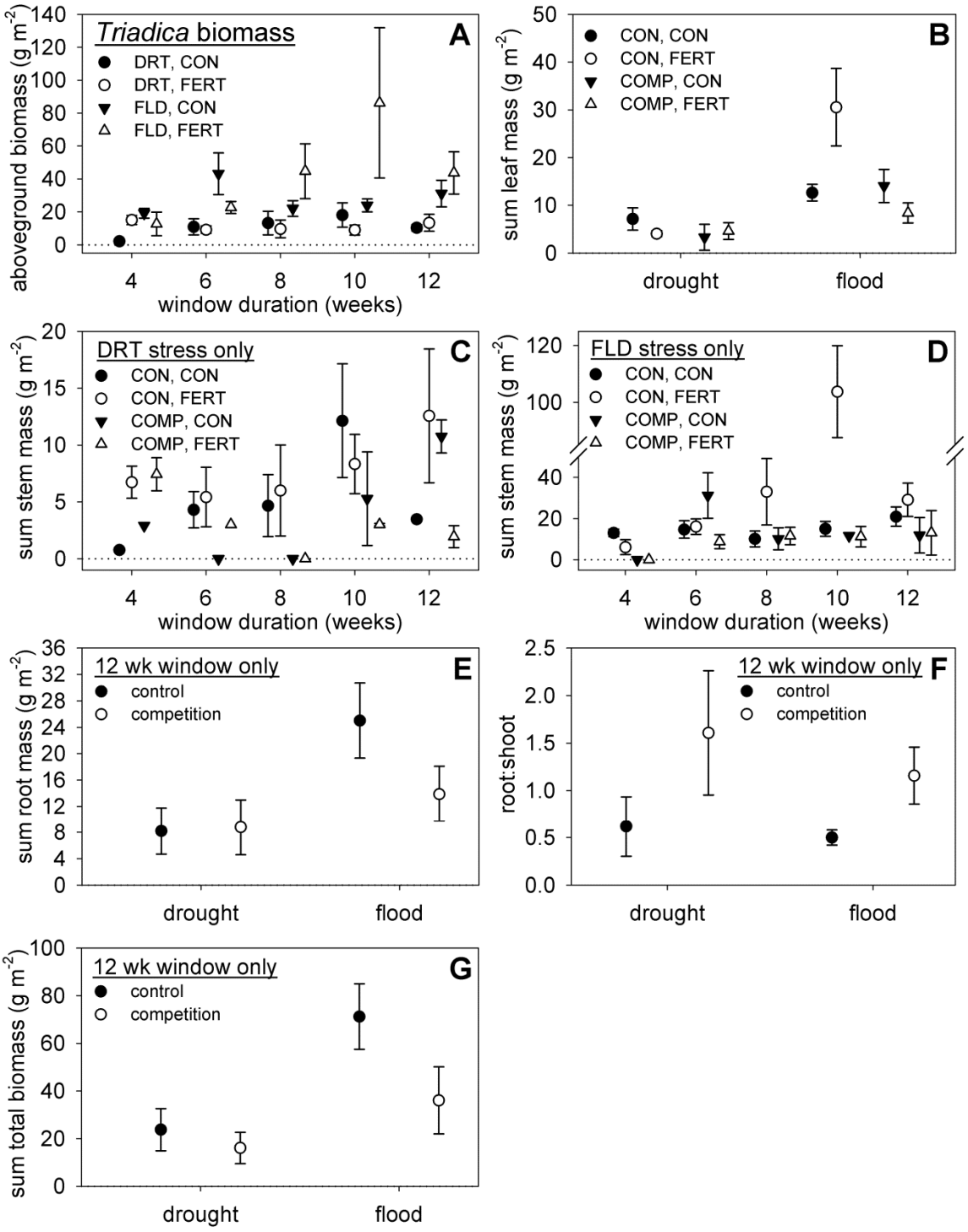

Figure 4.3. Effects of experimental treatments on six metrics of *Triadica* biomass. Panels represent biomass metrics (means ±1 SE) broken down by treatments that significantly affected that metric (except in B, where window duration is not represented

for clarity, and E-G, where several interesting but insignificant trends are shown). Legend: stress type – drought (DRT) or flood (FLD); competition – natives added (COMP) or control (CON); fertilization – NPK added (FERT) or control (CON). Pot sums of total aboveground *Triadica* biomass (A), leaf biomass (B) and stem biomass (C,D) were reduced in drought or competition treatments and generally greater among longer windows or with fertilization. However, fertilization only increased these biomass metrics in flood treatments but not consistently across window durations (win*stress*fert), and tended to decrease biomass when paired with competition (comp*fert). Competition had stronger effects on these biomass metrics among longer window durations (win*comp). For leaf biomass (B), the difference between flood and drought was greater among longer windows (win*stress) and competition had relatively stronger negative effects in flood versus drought (stress*comp). Sums of root (E) and whole plant biomass (G) were lower in drought treatments and tended to be lower with competition in flood treatments. F – Competition increased root:shoot ratios, which were surprisingly comparable between drought and flood treatments.

SUPPORTING INFORMATION

Table 4.S1. Results of repeated measures ANOVAs testing effects of experimental treatments on *Triadica* demography over time. Treatments include window duration (W), stress type (S), competition (C), fertilization (F), time (T) and their interactions. Abundance of *Triadica* seedlings was untransformed and sums of *Triadica* seedling heights and leaf abundances for each pot were square root transformed for analyses.

		abundance			sum of heights		sum of leaves	
factor	d.f.	F_{399}	*p*	d.f.	F_{110}	*p*	F_{110}	*p*
Window	4	2.6	**0.0333**	4	3.8	**0.0070**	3.2	**0.0183**
Stress	1	0.8	0.37	1	22.9	**0.0000**	34.6	**0.0000**
Comp	1	4.9	**0.0279**	1	0.9	0.35	5.2	**0.0250**
Fert	1	1.1	0.31	1	1.7	0.20	0.7	0.40
W*S	4	1.1	0.38	4	0.7	0.60	1.9	0.12
W*C	4	0.7	0.61	4	0.2	0.95	0.6	0.69
S*C	1	0.0	0.83	1	0.0	0.85	0.6	0.43
W*F	4	0.4	0.79	4	0.3	0.90	0.3	0.86
S*F	1	0.2	0.69	1	1.7	0.20	1.2	0.28
C*F	1	0.8	0.37	1	0.2	0.67	0.5	0.47
W*S*C	4	1.5	0.20	3	0.6	0.59	1.5	0.22
W*S*F	4	1.1	0.35	4	2.4	0.06	2.8	**0.0338**
W*C*F	4	0.6	0.64	4	0.4	0.81	0.6	0.69
S*C*F	1	0.0	0.88	1	0.4	0.52	0.2	0.67
W*S*C*F	4	0.4	0.80	2	1.7	0.19	1.3	0.28
factor	d.f.	F_{800}	*p*	d.f.	F_{222}	*p*	F_{222}	*p*
Time	2	2.3	0.10	2	25.3	**<0.0001**	18.1	**<0.0001**
W*T	8	0.9	0.50	8	1.9	0.06	2.7	**0.0084**
S*T	2	2.4	0.09	2	3.9	**0.0216**	7.2	**0.0010**
C*T	2	6.5	**0.0015**	2	22.0	**<0.0001**	12.8	**<0.0001**
F*T	2	0.3	0.77	2	0.2	0.79	0.2	0.78
W*S*T	8	1.2	0.31	8	1.2	0.27	1.1	0.33
W*C*T	8	1.2	0.32	8	0.9	0.52	0.8	0.57
S*C*T	2	7.8	**0.0004**	2	14.5	**<0.0001**	9.0	**0.0002**
W*F*T	8	0.4	0.94	8	0.4	0.94	0.3	0.96
S*F*T	2	1.6	0.20	2	1.3	0.27	1.4	0.24
C*F*T	2	1.1	0.33	2	0.6	0.53	1.0	0.38
W*S*C*T	8	1.1	0.36	6	2.2	**0.0445**	1.2	0.31
W*S*F*T	8	0.4	0.92	8	0.4	0.93	0.6	0.76
W*C*F*T	8	1.0	0.43	8	1.4	0.21	1.2	0.32
S*C*F*T	2	1.6	0.20	2	0.2	0.82	0.2	0.81
W*S*C*F*T	8	1.0	0.40	4	2.3	0.06	1.6	0.17

Table 4.S2. Results of ANOVAs testing effects of experimental treatments on absolute changes (Δ) in *Triadica* performance. Treatments include window duration (W), stress type (S), competition (C), fertilization (F) and their interactions. Absolute changes (final – initial; Δ) in sums of *Triadica* seedling heights and leaf abundances for each pot were untransformed for analyses. Initial values were measured immediately before we initiated water stress (pre-stress). Final values were measured after 56 days of either drought or flood stress (post-stress).

		Δ sum of heights		Δ sum of leaves	
factor	d.f.	F_{121}	*p*	F_{121}	*p*
Window	4	2.2	0.07	4.4	**0.0028**
Stress	1	6.8	**0.0107**	13.3	**0.0004**
Comp	1	23.5	**<0.0001**	11.7	**0.0009**
Fert	1	0.1	0.76	0.0	0.87
W*S	4	1.7	0.15	1.6	0.19
W*C	4	1.1	0.34	0.1	0.99
S*C	1	5.4	**0.0227**	5.1	**0.0262**
W*F	4	0.8	0.55	0.5	0.74
S*F	1	4.8	**0.0314**	1.3	0.26
C*F	1	1.8	0.19	2.4	0.12
W*S*C	3	2.6	0.06	1.2	0.32
W*S*F	4	0.6	0.64	0.5	0.70
W*C*F	4	1.8	0.14	1.4	0.22
S*C*F	1	0.4	0.55	0.9	0.35
W*S*C*F	2	3.5	**0.0360**	1.5	0.23

Table 4.S3. Results of ANOVAs testing effects of experimental treatments on native plant abundance and performance. Treatments include window duration (W), stress type (S), fertilization (F) and their interactions. These tests only consider pots subject to the competition treatment because native plants were weeded from non-competition pots; hence competition is not considered as a factor here. Pre-stress and final native plant percent cover were arcsine transformed, pre-stress and final maximum native plant height were untransformed, aboveground native plant biomass was square root transformed, and absolute changes (Δ) in cover and maximum height during stress were untransformed for analyses.

		pre-stress percent cover		final percent cover		pre-stress max height		final max height		aboveground biomass		Δ percent cover		Δ max height	
factor	d.f.	F_{199}	*p*	F_{199}	*p*	F_{199}	*p*	F_{199}	*p*	F_{199}	*p*	F_{199}	*p*	F_{197}	*p*
Window	4	5.1	**0.0006**	9.7	**<0.0001**	19.5	**<0.0001**	14.6	**<0.0001**	10.2	**<0.0001**	27.1	**<0.0001**	11.2	**<0.0001**
Stress	1	1.7	0.20	60.9	**<0.0001**	0.0	0.92	2.8	0.09	4.5	**0.0351**	83.3	**<0.0001**	3.8	0.05
Fert	1	0.0	0.90	0.3	0.60	1.7	0.19	0.4	0.55	2.6	0.11	0.5	0.47	0.4	0.52
W*S	4	1.5	0.21	10.3	**<0.0001**	1.1	0.34	2.7	**0.0336**	4.0	**0.0039**	3.6	**0.0081**	3.5	**0.0083**
W*F	4	0.5	0.74	1.5	0.20	0.1	0.97	1.4	0.24	1.6	0.18	0.7	0.60	1.5	0.21
S*F	1	1.2	0.28	0.4	0.51	0.1	0.75	0.5	0.50	0.0	0.93	0.6	0.45	0.2	0.65
W*S*F	4	0.6	0.65	2.6	**0.0397**	1.1	0.38	1.7	0.16	1.1	0.38	0.5	0.72	1.3	0.28

Table 4.S4. Results of repeated measures ANOVAs testing effects of experimental treatments on native plant demography over time. Treatments include window duration (W), stress type (S), fertilization (F), time (T) and their interactions. These tests only consider pots subject to the competition treatment because native plants were weeded from non-competition pots; hence competition is not considered as a factor here. Native plant percent cover was arcsine transformed and maximum native plant height was untransformed for analyses.

		percent cover		max height	
factor	d.f.	F_{199}	*p*	F_{199}	*p*
Window	4	2.1	0.08	15.1	**<0.0001**
Stress	1	6.8	**0.0101**	0.2	0.68
Fert	1	0.0	0.97	1.0	0.31
W*S	4	3.0	**0.0188**	1.8	0.13
W*F	4	1.0	0.42	0.5	0.70
S*F	1	1.4	0.24	1.0	0.33
W*S*F	4	1.2	0.30	1.4	0.25
factor	d.f.	F_{400}	*p*	F_{400}	*p*
Time	2	19.7	**<0.0001**	6.3	**0.0021**
W*T	8	16.6	**<0.0001**	12.2	**<0.0001**
S*T	2	52.4	**<0.0001**	7.7	**0.0005**
F*T	2	0.4	0.67	0.4	0.68
W*S*T	8	4.7	**<0.0001**	3.4	**0.0008**
W*F*T	8	0.5	0.87	1.5	0.17
S*F*T	2	0.4	0.64	2.2	0.12
W*S*F*T	8	0.6	0.76	1.4	0.18

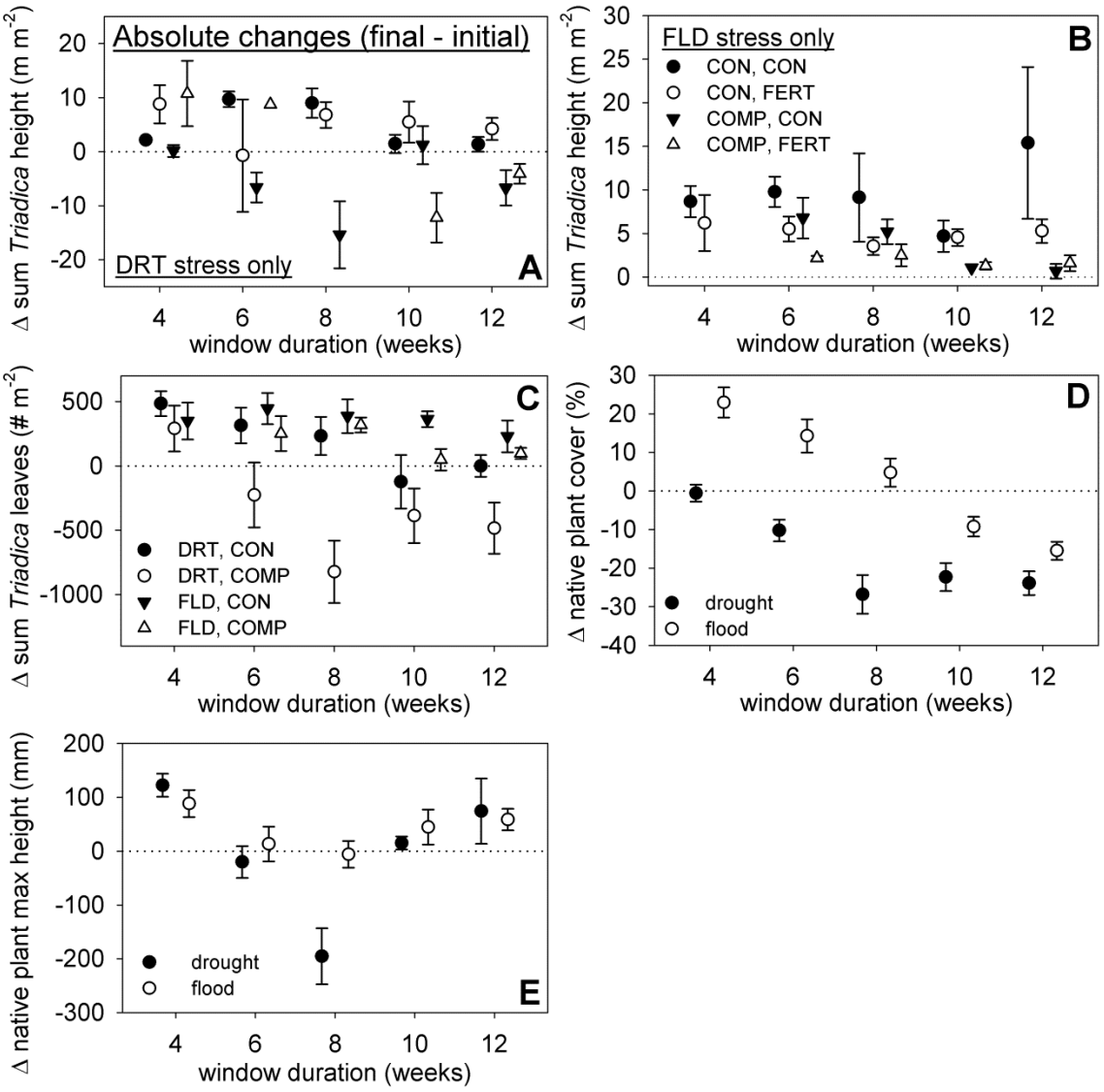

Figure 4.S1. Effects of experimental treatments on absolute changes in *Triadica* and native plant performance. Panels represent performance metrics (means ±1 SE) broken down by treatments that significantly affected that metric. Legend: stress type – drought (DRT) or flood (FLD); competition – natives added (COMP) or control (CON); fertilization – NPK added (FERT) or control (CON). Absolute changes (Δ) during stress in pot sums of *Triadica* seedling heights (A,B) and leaf abundances (C) were lower and sometimes negative in drought stress and generally lower with competition; negative effects of competition were stronger with drought (stress*comp). Fertilization reduced

the magnitude of changes in *Triadica* height during flood stress but increased the magnitude of changes during drought stress (stress*fert; A,B). *Triadica* gained fewer leaves in longer window duration treatments (C). D – Absolute changes in native plant cover were lower and generally negative among longer window duration treatments and were lower and typically negative in drought stress. Negative impacts of drought were weaker among longer window durations (win*stress). E – Changes in height were lower and sometimes negative among intermediate window durations, and the effects of drought were more negative among intermediate window durations (win*stress).

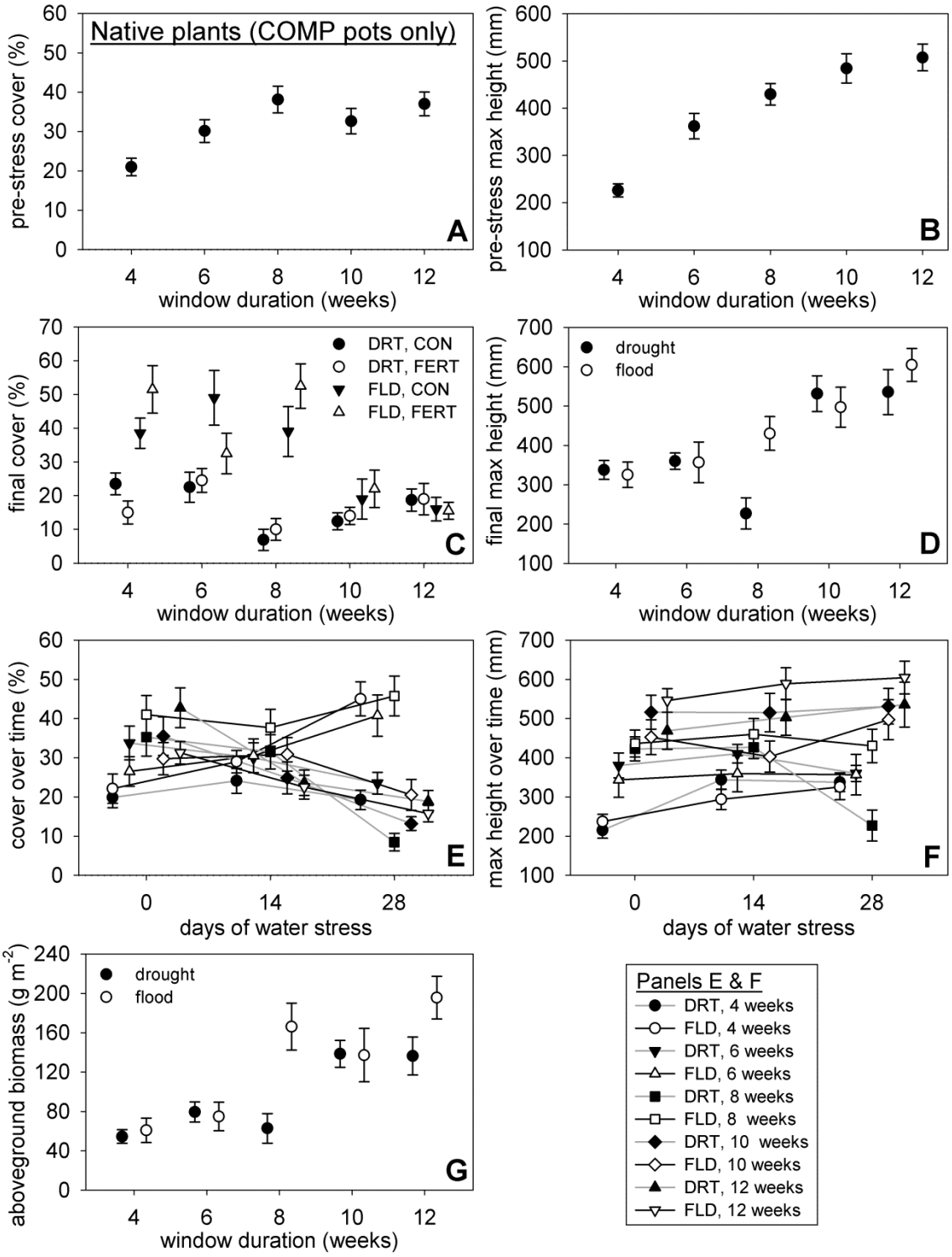

Figure 4.S2. Effects of experimental treatments on native plant demography. Each panel represents one metric of native plant demography (means ±1 SE) broken down by treatments that significantly affected that metric. Legend: stress type – drought (DRT) or

flood (FLD); fertilization – NPK added (FERT) or control (CON). Only pots with the competition treatment are considered because native plants were weeded in non-competition treatments. Pre-stress native plant percent cover (A) and maximum height (B) were greater among longer window duration treatments. C – Final native plant percent cover was lower among longer window durations and generally lower in drought stress, but the difference between flood and drought was inconsistent and insignificant among the longest window durations (win*stress). D – Final maximum native plant height was higher among longer window durations; native height was greater in flood stress in the 8 week window duration treatment only. E – Native plant cover generally decreased over time during stress (win*time) and was lower with drought stress at later surveys (stress*time), but increased among shorter window duration treatments during flood stress only (win*stress*time). F – Maximum native plant height over time was higher among longer window duration treatments (win*time) and generally increased during flood stress but often decreased or did not change during drought stress (stress*time). G – Native plant aboveground biomass was higher among longer window durations; native biomass was greater in flood stress in 8 and 12 week window duration treatments only.

CHAPTER FIVE

Impacts of propagule availability and soil moisture variation on restoration outcomes in eleven habitats invaded by Chinese tallow tree along a moisture gradient

Impacts of propagule availability and soil moisture variation on restoration outcomes in eleven habitats invaded by Chinese tallow tree along a moisture gradient

ABSTRACT

Invasion success of both native and exotic species is hypothesized to depend upon propagule availability, environmental suitability and biotic interactions in recipient ecosystems. We expect that reinvasion pressure, which is the rate of increase in new exotic prevalence following removal of conspecific adults, depends on the same factors and mechanisms. Reinvasion pressure governs outcomes and costs of restoration and exotic plant control but is highly variable and poorly understood.

To better understand the factors driving invasion and succession during restoration, we quantified the impacts of propagule availability of native and exotic plant species and variation in soil moisture within eleven replicated experimental restoration sites in southeast Texas. Sites represent a broad moisture gradient and were dominated by *Triadica sebifera* (Chinese tallow tree, a major invader) prior to manipulation.

We found propagule availability was most important to reinvasion pressure where abiotic conditions were favorable for *Triadica*, but temporal availability of suitable abiotic conditions was most important to reinvasion where conditions were more extreme. Intermediate moisture conditions, less intense or less frequent water stress, and higher soil N increased reinvasion pressure. Native seed addition (i.e. increased competition) decreased *Triadica* survival in some sites and generally reduced *Triadica*

performance. In sites where *Triadica* generally performed well, individual survival and performance of trees (aged two years maximum) were remarkably high in 2011 during the worst drought ever recorded in Texas. However, despite initial *Triadica* dominance across sites, minimal post-removal management was required for successful restoration in six of eleven sites.

Native plant diversity, abundance and community structure varied widely among sites. Propagule availability was only important to some functional groups in some places. Overall, native plant success was negatively correlated with *Triadica* prevalence and generally any factors that promoted *Triadica* success. This suggests invaders can negatively impact native communities very early in succession and substantiates potential merits of destructive exotic management during restoration.

Our results provide strong support for the 'outgrow the stress' hypothesis and largely validate many of its specific predictions. This work establishes that we can use niche-based models to predict variation in average reinvasion pressure, and thus outcomes and costs of restoration and exotic management, by considering fluctuations in both local abiotic conditions and abiotic tolerances of invaders. Niche-based reinvasion models can improve restoration efficacy and efficiency in invaded habitats by informing optimal management strategies and site selection.

INTRODUCTION

Invasion is a fundamental part of community assembly and succession (Connell and Slatyer 1977), but invasions of noxious exotic species are a foremost threat to global biodiversity and ecosystem function (D'Antonio and Vitousek 1992, Mack et al. 2000, Sakai et al. 2001). Adult populations may crash for many reasons (e.g. fire, disease, displacement by exotics species, or herbicide application), and reestablishment or reinvasion is theoretically governed by the same factors that influence initial establishment success (Gabler and Siemann 2012). Specifically, propagule availability (Simberloff 2009), local abiotic conditions (e.g. climate or nutrient concentrations; Kolar and Lodge 2001), and positive and negative biotic interactions (Maron and Connors 1996, Tilman 2004) are particularly important to establishment during invasion.

Reinvasion is a principal challenge when restoring ecosystems dominated by invasive exotic plants and during eradication or control efforts (Buckley et al. 2007). In this context, 'reinvasion pressure' is the rate of new exotic recruitment following removal of a (dominant) population of conspecific adults. Reinvasion pressure is crucial to the outcomes and costs of restoration and control efforts because an exotic's prevalence governs the strength of its impacts (Grime 1998) and the methods required to successfully control it, and methods differ in their costs (Epanchin-Niell and Hastings 2010) and impacts on native species (Mason and French 2007, Rinella et al. 2009). Reinvasion pressure can vary broadly among habitats dominated by the same species, but the mechanisms driving this variation are poorly understood (Buckley et al. 2007, Kettenring and Adams 2011, Gabler and Siemann 2012).

The primary goal of ecological restoration is rehabilitation of functional native communities, and controlling invaders is only one aspect of this process (Suding et al. 2004, Hulme 2006). Where exotics dominate, endemic plant species are less abundant, present only as seeds or locally extinct (D'Antonio and Vitousek 1992, Mack et al. 2000). Reestablishment of historic native plant abundances rely on an essentially identical reinvasion process governed by the same factors of propagule availability (Hutchings and Booth 1996, Seabloom and van der Valk 2003), abiotic conditions relative to species requirements (Bunn and Arthington 2002, Zedler and Kercher 2005), and positive (Vieira et al. 1994, Ashton et al. 1997) and negative interspecific interactions (Tilman 2004, Kettenring and Adams 2011). Thus the reinvasion pressure concept validly applies to native species, but native reestablishment success also varies within and among species and is poorly understood (Seabloom and van der Valk 2003, Zedler and Kercher 2005).

We previously developed the 'outgrow the stress' hypothesis (Gabler and Siemann 2012) to explain variation in reinvasion pressure and began experimentally validating its key predictions using invasive *Triadica sebifera* (Chinese tallow tree) as a model. We proposed that reinvasion pressure is ultimately governed by spatiotemporal availability of propagules and 'realized recruitment windows,' which are periods of variable duration permitting new exotic establishment, and are defined by abiotic conditions and biotic interactions. Crucially, how often "preparation meets opportunity" differs both among sites and within sites from year to year. However, differences between sites in average reinvasion pressure can become masked by exotic dominance if increases in niche breadth during development and sufficient longevity enable exotics to persist in sites where recruitment opportunities range from frequent to highly episodic.

Existing invasion hypotheses (e.g. Grubb 1977, Harper 1977, Johnstone 1986, Chesson 2000, Shea and Chesson 2002, Tilman 2004) commonly emphasize spatiotemporal variation in abiotic conditions and biotic interactions, but 'outgrow the stress' uniquely emphasizes ontogenetic changes in invader responses to these conditions and interactions (Gabler and Siemann 2012).

In support of this hypothesis, we demonstrated that *Triadica* exhibits rapid increases in the breadth of its moisture niche early in development (Chapter Three). This substantially increased seedling survival and performance in conditions unsuitable for germination and may explain how adult persist in such conditions. We next demonstrated at a population level that longer periods of favorable moisture conditions prior to water stress (window duration) increased *Triadica* abundance, survival and performance through a subsequent period of water stress, but competition with native grasses reduced these metrics (Chapter Four). Fertilization generally enhanced *Triadica* performance but did not affect abundance or survival, and interactions among these factors and with stress type (drought or flood) often mitigated, enhanced or reversed the effects of particular treatments on survival or performance in specific environmental contexts.

We know that propagule availability, abiotic conditions and biotic interactions are particularly important to reinvasion pressure, but their relative impacts are unclear and likely vary among sites and over time. These factors often interact, and extremes in one may be able to "trump" other factors in certain circumstances (Chapter Four). For example, intense climate could prevent reinvasion despite abundant propagules and weak competition (Shea and Chesson 2002), but optimal climate means nothing without sufficient propagules (Simberloff 2009).

To better understand how propagule availability, abiotic conditions and biotic interactions influence reinvasion pressure, we performed replicated restoration experiments manipulating native and *Triadica* seed abundances and soil moisture in 11 sites along a moisture gradient in southeast Texas that were previously dominated by *Triadica*. This multi-site field experiment further tests three central sub-hypotheses of the 'outgrow the stress' framework explaining how these key factors drive reinvasion:

Propagule availability hypothesis – Reinvasion pressure will scale with propagule abundance but plateau when propagule density reaches spatial saturation (i.e. seedlings are subject to immediate self-thinning). However, the effects of propagule abundance will decrease as abiotic stress increases.

Abiotic niche hypothesis – Reinvasion pressure will be a function of local environment, peaking at environmental optima and decreasing as conditions diverge from these optima. Very low propagule abundance will override environmental effects, and interspecific interactions will mediate abiotic effects on reinvasion depending on the parameter and type of interaction.

Interspecific interactions hypothesis – Competition will reduce and facilitation will increase reinvasion pressure. Both factors should operate and net effects will depend on local resource availability relative and stress intensity, but we generally expect an overall net negative effect due to competition. *Triadica* will top the competitive hierarchy.

Greater understanding of what drives variation in reinvasion pressure will enhance our general understanding of community assembly and succession, and will improve niche- and climate-based predictions of recruitment success for key species (e.g.

dominant exotics). Such predictions would be valuable decision making tools that could increase restoration efficiency by informing site selection and optimal management strategies (Gabler and Siemann 2012).

METHODS

Focal species

Chinese tallow tree [*Triadica sebifera* (L.) Small, Euphorbiaceae; synonym *Sapium sebiferum*] has been broadly introduced and is a major invasive species in the southeastern United States (Bruce et al. 1997). *Triadica* invades grasslands (including endangered coastal prairies), freshwater wetlands and forests and can form monocultures within two decades (Bruce et al. 1997, Harcombe et al. 1999). *Triadica* exhibits high growth rates (Lin et al. 2004), high fecundity (Renne et al. 2000), broad abiotic tolerances (Jones and McLeod 1989, Butterfield et al. 2004) and low herbivore loads in its introduced range (e.g. Siemann and Rogers 2003). *Triadica* seeds can remain viable for 5-7 years (Bruce et al. 1997, Cameron et al. 2000) and require oscillating day-night temperatures characteristic of exposed soil to cue germination (Nijjer et al. 2002, Donahue et al. 2004, 2006), as well as moist but unsaturated soils, which are optimal for seedling survival and growth (Chapter Three). Established *Triadica* juveniles have broad moisture tolerances (Hall and Harcombe 1998, Butterfield et al. 2004), but newly germinated seedlings have narrow tolerances that rapidly broaden to enable persistence in conditions ranging from constant flooding to short-term drought (an ontogenetic moisture niche expansion) within months of germination (Chapter Three).

Multi-site replicated restoration experiment

In March-April 2009 we identified 11 sites in southeastern Texas that were heavily dominated by *Triadica* and represented a broad gradient of average soil moisture. Individual sites were located within three venues: Justin Hurst Wildlife Management Area (JH) near Jones Creek in Brazoria County (28°56'55.86" N, 95°26'16.64" W), Katy Prairie Conservancy (KP) near Katy in Waller County (29°56'2.06" N, 95°53'37.71" W), and University of Houston Coastal Center (UH) near La Marque in Galveston County (29°23'24.75" N, 95°2'37.04" W). See Table 5.S1 for precise locations of each study site.

We began our experimental restorations by removing all adult and juvenile *Triadica* trees within a 25 x 25 m plot at each of the 11 study sites using standard mulching and herbicide methods. A professional operator performed the mulching from 28 April to 2 May 2009, and used a rubber-tracked ASV Posi-Track skid loader (Terex ASV, Grand Rapids, Minnesota, USA) mounted with a FAE 200U forestry mulching head (FAE USA Inc., Flowery Branch, Georgia, USA) to fell and grind all *Triadica* into course mulch which we left in place. We applied Garlon 4 Ultra herbicide (triclopyr; Dow AgroSciences LLC, Indianapolis, Indiana, USA) diluted in bark oil to any surviving stumps from 6-17 July 2009 and again from 16-30 September 2009 using a backpack sprayer, which permitted highly precise application directly to stumps.

From 4-21 May 2009, we established 48 mesocosm pots (19.6 L, 25 cm tall, 35.6 cm top diameter) within a randomly selected quadrant of each study site (n = 528 pots). We spaced pots one meter apart along a 7 x 7 grid (this provided an “extra space” that allowed us to avoid unusual terrain or large rootstocks), and randomly assigned

experimental treatments to pots. We installed pots by drilling holes ~25 cm deep using a 36 cm auger head mounted on a rubber-tracked S600TX compact skid loader (Vermeer Corporation, Pella, Iowa, USA). We filled each mesocosm pot with soil from its assigned space up to the drainage holes 5 cm below the lip, which we previously drilled in the sides of pots so that water could drain to or from the soil surface within pots. We reallocated extra soil as needed to adjust the relative height of each pot according to its moisture treatment.

The experiment utilized a 3x2x2 full factorial design (12 treatment combinations with 4 replicates per site) manipulating soil moisture and abundance of *Triadica* and native seeds. We established three passive moisture treatments by adding side drainage (described above) and positioning pots at different heights relative to the ground so soil surfaces within pots were as follows: 'wet' – 5 cm below ground, 'ambient' – level with ground, or 'dry' – 5 cm above ground. Our intention was to direct precipitation into or out of a given pot, or not to direct flow. This approach was (necessarily) highly economical and did influence moisture as intended, but it also altered microtopography. Nevertheless, this allowed us to decouple moisture from other site characteristics. We established two *Triadica* seed addition treatments: 'TSA' – 10 *Triadica* seeds added per pot, or 'control' – no addition; and two native seed addition treatments: 'NSA' – 2.5 g of native seed mix added per pot, or 'control' – no addition. The native mix included Texas-native species spanning a broad range of moisture niches (e.g. wetland indicator statuses ranged from obligate upland to obligate wetland; Appendix 5.S1). We used 2.5 g of native mix because that was the approximate mass of 10 *Triadica* seeds. To

synchronize planting, we added seeds once all pots were established from 21-23 May 2009.

We built barb-wire fences around sites accessible by cattle from 25-29 May 2009 using a 3-strand design that deters cattle but does little to prevent access by other large mammals, such as deer or feral hogs (we saw evidence of both within some fenced plots). Fences did not prevent access by smaller mammals, such as rabbits or squirrels. We quantified soil total N content for each study site via flash combustion/gas chromatography using soil samples collected between 19 May-11 June 2010 from remnant stands of tallow immediately adjacent to each study plot.

We surveyed pots every October from 2009-2011. In 2009 we counted live and dead *Triadica* seedlings and estimated percent cover of native plant functional groups. In 2010 we performed the prior, measured height and leaf abundance of *Triadica* seedlings, and tagged *Triadica* seedlings by cohort. Surveys in 2011 included the prior and quantified native cover by species. We harvested aboveground biomass by species after final surveys. Biomass was oven dried at 70°C for 48-96 hours and weighed. We measured soil moisture in pots once in 2009, four times in 2010 and 1-2 times in 2011 using a FieldScout TDR 300 soil moisture meter (Spectrum Technologies, Inc., Plainfield, Illinois, USA). We quantified moisture another 1-2 times in 2011 via gravimetric methods. We measured depth at each moisture reading and twice in 2009. Our average moisture and depth metrics are the means of annual averages.

To evaluate effects of experimental treatments and environmental factors on *Triadica* and native plant reinvasion pressure, we fit all response variables using Generalized Linear Models (GLMs) in R version 2.15 using the ‘glm’ command (R

Foundation for Statistical Computing, Vienna, Austria). This allowed us to build models using Poisson and binomial distributions, which are most appropriate for response variables comprising count (e.g. *Triadica* abundance) or proportion data (e.g. *Triadica* survival), respectively. This approach also uses maximum likelihood estimation of parameters, which is most appropriate for our comparisons of survival among treatments because natural variation resulted in unbalanced sample sizes (Bolker et al. 2009). Model terms included average soil moisture, minimum soil moisture, average water depth and soil total N content as covariates, and venue, site, moisture treatment, tallow seed addition (TSA), native seed addition (NSA), and all possible interactions of moisture, NSA and TSA as categorical predictors. Site was nested within venue, and moisture, TSA, NSA and their interactions were nested within site.

We performed ANCOVA F-tests for each normally-distributed response variable and ANODEV (analysis of deviance, a form of likelihood-ratio testing) chi-squared tests for each Poisson- or binomially-distributed response variable. We used Type I Sums of Squares in our ANCOVAs and an equivalent approach in our ANODEVs, which are preferable for nested designs like ours, so the order of variables does matter. We utilized Holm-Bonferroni adjusted pairwise t-tests for post-hoc testing of differences between treatment means and ordinary least squares regressions to evaluate relationships between variables not considered in our GLMs. Native percent cover values were arcsine transformed to better meet the assumptions of normality; no other transformations were necessary.

RESULTS

Moisture treatments had the intended effects. Average soil moisture, average water depth and minimum moisture were higher in 'wet' pots and lower in 'dry' pots (Table 5.S2). Moisture metrics also depended heavily on venue and site (Table 5.S2), and, in some cases, this variation was considerably greater than that produced by our manipulations. We note that the most severe drought ever recorded in Texas occurred during the 2011 growing season. This surely impacted our results, but all sites were affected, so the drought did relatively little to complicate their interpretation.

Triadica germination depended on venue, site, moisture treatment, native seed addition (NSA), *Triadica* seed addition (TSA), and the moisture*NSA and moisture*NSA*TSA interactions (Table 5.1, Figure 5.1). Moisture treatment effects varied by venue and site (Figure 5.1A). In wet pots, germination was reduced in JH Fire N and S, lower relative to dry pots in JH Tank N, and higher than ambient pots in UH Pipe N. Germination was considerably higher in dry pots in UH Can W. Overall, more *Triadica* germination was observed in dry pots and less in wet pots compared to ambient pots (Figure 5.1D). TSA consistently increased *Triadica* germination but its effect strength varied by site (Figure 5.1B). NSA did not affect *Triadica* germination in most sites, but decreased it in JH Fire S and increased it in UH Can W (Figure 5.1C). NSA also dampened differences in germination among moisture treatments (moisture*NSA interaction; Figure 5.1D). Cumulative *Triadica* germination was positively correlated with average and minimum soil moisture and soil total N, and negatively correlated with average depth in our model (Table 5.1, Figure 5.1E-H). However, more variance was explained by quadratic relationships between germination and average or minimum

moisture (Figure 5.1E-F), and the relationship with average depth was insignificant independent of the other covariates (Figure 5.1G).

Triadica abundance was influenced by venue, site, moisture treatment, *Triadica* seed addition (TSA), and the moisture*TSA interaction (Table 5.1, Figure 5.2). Moisture treatment effects varied in strength and direction by venue and site (Figure 5.2A). Abundance in wet pots was lower across JH but higher in KP War E, whereas abundances were similar among moisture treatments in all UH sites (high overall) and in KP Levee and KP War W (very low overall). TSA typically increased final *Triadica* abundance, but not in all sites, and effect strengths differed considerably where the increase was significant (Figure 5.2B). Overall, abundance was greater in dry than wet treatments, but abundances in ambient pots were similar to dry pots with TSA and similar to wet pots without TSA (moisture*TSA; Figure 5.2C). Abundance followed the same general environmental patterns as germination, correlating positively with average (Figure 5.2D) and minimum moisture (Figure 5.2E) and soil N (Figure 5.2G), and negatively with average depth (Figure 5.2F). Quadratic relationships between abundance and average or minimum moisture (Figure 5.2D-E) or soil N (Figure 5.2G) explained more variance than linear ones, and the relationship with average depth was insignificant without other covariates (Figure 5.2F).

Overall *Triadica* survival (final abundance / cumulative germination) depended on venue, site, moisture treatment, TSA and NSA (Table 5.1, Figure 5.3). In the few sites where moisture treatments affected survival, their effects varied in strength and direction by venue and site. Survival was reduced in wet pots in JH Fire S, but higher in wet pots in KP War E and UH Can W (Figure 5.3A). TSA had no effect in most sites, but

increased *Triadica* survival in JH Tank S and UH Can W and decreased survival in JH Fire N (Figure 5.3B). NSA decreased survival overall, but had no effect in most sites and increased survival in JH Fire S (Figure 5.3C). Survival was positively correlated with average and minimum moisture and negatively correlated with average depth, but independent of soil N in our GLM (Figure 5.3D-G). However, regressions of survival with individual abiotic factors suggest the relationship with soil N is significant (Figure 5.3G), that quadratic relationships with average moisture (Figure 5.3D) and soil N (Figure 5.3G) explain considerably more variance than linear models, and that the negative correlation with average depth is marginally insignificant (Figure 5.3F).

Aboveground *Triadica* biomass per pot depended on moisture and TSA treatments and the NSA*TSA interaction (Table 5.2, Figure 5.4). Biomass was uniquely independent of venue and site and uncorrelated with average soil moisture in our GLM. Nevertheless, there were large differences among sites in *Triadica* biomass. In the four sites where moisture affected biomass (JH Tank N and S, UH Can E and W), biomass was lower in wet pots than in dry and/or ambient pots (Figure 5.4A). TSA increased biomass in three of the same four sites but in no others (Figure 5.4B). Biomass was higher in TSA pots; NSA significantly reduced biomass with TSA but had no effect in pots without TSA where biomass was lowest (Figure 5.4C). *Triadica* biomass correlated positively with minimum moisture (Figure 5.4E) and soil N (Figure 5.4G) and negatively with average depth (Figure 5.4F) in our GLM. Independent of other covariates, biomass had a significant quadratic relationship with average moisture but no linear relationship (Figure 5.4D).

Native species richness depended on venue, site, moisture and NSA treatments and the moisture*NSA*TSA interaction (Table 5.1; Figure 5.5). In eight sites, native richness increased in dry pots or decreased in wet pots relative to other moisture treatments (Figure 5.5A). NSA increased native plant richness in JH Fire S, JH Tank N and UH Can E but most often had no effect (Figure 5.5B). In dry pots, native richness was greater in pots with NSA and TSA than in those without either (moisture*NSA*TSA), and richness was lower in wet pots without NSA than in dry and ambient pots regardless of seeding treatments (moist*NSA; Figure 5.5C). In our GLM, native richness was negatively correlated with average (Figure 5.5D) and minimum moisture (Figure 5.5E) and soil N (Figure 5.5G) but independent of average depth (Table 5.1). However, native species richness was negatively correlated with average depth in a simple linear regression (Figure 5.5F).

Patterns of native species diversity (Shannon index, *H'*) closely mirrored those of native species richness overall and within sites, and thus are not shown. The only relevant difference being that moisture*NSA was the only interaction to affect native diversity, and it did so as described above. Native diversity followed the same environmental patterns as richness.

Total native biomass depended on venue, site and the NSA*TSA interaction (Table 5.2). Total biomass peaked in UH Pipe S and was highly variable at this site, where native woody biomass of *Myrica cerifera* L. and especially *Sesbania drummondii* (Rydb.) Cory were uniquely high (Figure 5.6A). Total native biomass was lower and less variable in pots without NSA or TSA than all other seeding treatments, which were

comparable and highly variable (Figure 5.6B). Total biomass weakly correlated positively with soil N (Table 5.2).

Native graminoid biomass was influenced by venue, NSA, TSA and the NSA*TSA interaction (Table 5.2). Graminoid biomass was highest in JH, especially JH Tank N, and varied considerably among sites even though site was not significant in our GLM (Figure 5.6C). Graminoid biomass was higher in pots with NSA and without TSA, but largely because it was considerably higher (and more variable) in pots with NSA only (NSA*TSA; Figure 5.6D). Apart from a marginally significant negative relationship with minimum moisture, graminoid biomass did not correlate with any environmental metrics (Table 5.2).

Forb biomass depended on site, moisture, NSA and TSA treatments and moisture*NSA, moisture*TSA and moisture*NSA*TSA interactions (Table 5.2). Forb biomass peaked in KP Levee (Figure 5.6E) and was affected differently by particular seed addition treatments in different moisture treatments (Figure 5.6F). Forbs biomass was lower in ambient pots than in dry or wet pots, which were comparable. In ambient pots, NSA plus TSA increased forb biomass. In wet pots, forb biomass was higher with only TSA than with neither TSA nor NSA. In dry pots, forb biomass was higher with NSA plus TSA or neither than with only NSA or only TSA.

Native woody species were generally rare. Their biomass depended on venue, site and the NSA*TSA interaction, and was weakly positively correlated with soil N (Table 5.2). These patterns were largely driven by the aforementioned woody prevalence in UH Pipe S. Biomasses of vines and other native plants were independent of all treatments and

covariates (Table 5.2). Figure 5.S1 provides a graphical summary of native plant coverage by functional group and total *Triadica* and native biomasses for each site.

DISCUSSION

We investigated the mechanisms driving reinvasion pressure during restorations of exotic-dominated habitats via a multi-site field experiment that manipulated soil moisture and native and exotic propagule availability within eleven replicated restorations of sites dominated by invasive *Triadica sebifera* (Chinese tallow tree). Our results provide the most compelling evidence to date of the broad variability in reinvasion pressure exhibited by an invasive exotic plant during restoration of sites it previously dominated. Our results are consistent with the 'outgrow the stress' hypothesis and validate many of its specific predictions, though not all aspects of the hypothesis that distinguish it from other spatiotemporal niche-based invasion hypotheses were clearly demonstrated here. Specifically, unequivocally demonstrating the importance of ontogenetic niche expansions in permitting establishment in marginal and extreme environments will likely require significantly more frequent (and perhaps longer-term) observations of environmental conditions and associated plant demographic responses. Nevertheless, we did observe patterns that suggest niche expansions in *Triadica* are important to its (re)invasion in relatively stressful habitats.

What matters where? Linking factors and environments

Venues and sites varied considerably in their abiotic environments, and most of our response variables were correlated with one or more environmental factors, so local environment should help explain site-specific treatment effects and variation among sites in general. Recall that our four metrics of *Triadica* reinvasion pressure (germination, abundance, survival and biomass) demonstrated highly consistent relationships with our environmental covariates, namely positive and/or unimodal relationships with average and minimum soil moisture and soil N, and negative or insignificant relationships with average depth. If we can identify the thresholds for environmental context-specific effects of key factors, we will be substantially more able to predict reinvasion pressure and restoration outcomes based on individual site characteristics.

Katy Prairie (KP) sites were relatively extreme environments and *Triadica* performed poorly under high abiotic stress. KP sites had sandy soils, the lowest average (13-15% saturation) and minimum moistures (5-7%), the lowest soil N (0.08-0.09%), and never flooded. TSA increased germination across KP sites, but abundance and biomass were unaffected by TSA in KP Levee and KP War W because survival was near zero, the lowest of all sites. However, in KP War E the wet moisture treatment increased survival and abundance, as one would expect in very dry sites. Together these results strongly suggest that seedling mortality due to insufficiently long periods of soil moisture suitable for establishment was overriding propagule availability to ultimately limit reinvasion pressure in KP sites. Notably, near zero germination without TSA suggests propagule availability would limit reinvasion in KP if favorable conditions arose. As a result, all metrics of *Triadica* reinvasion were lowest in KP sites. NSA also had no effect, as expected where conditions are unsuitable regardless of competition. Native plants

performed relatively well here (forb biomass peaked in KP Levee), and successful restoration in KP sites will likely require minimal *Triadica* management because our results suggest *Triadica* establishment is episodic. These sites may represent "cryptic opportunities" for cheap and easy restoration hypothesized and described in Chapter Three.

Conversely, the sandy Justin Hurst WMA sites (JH Tank N and S) exhibited the least water stress and the highest individual *Triadica* performance. They had intermediate average moistures (~27%) and moderate to high soil N (0.20-0.28%), but the highest minimum moistures (20-21%) and never flooded. TSA increased *Triadica* germination, abundance, biomass and, in JH Tank N, survival. These increases in abundance and biomass with TSA were the largest observed, and survival was higher only in UH Pipe S. *Triadica* biomass was 50-150% greater in Tank N (90.5 g) and Tank S (150.6 g) than the next highest sites, UH Can E and W (58.3 and 61.5 g, respectively), despite having fewer individuals. Notably, NSA reduced *Triadica* survival from 56% to 35% and biomass from 120.7 g to 57.7 g in JH Tank N overall, and NSA reduced biomass in TSA treatments in both JH Tank sites. Moisture conditions do not appear limiting, although divergences could reduce success as suggested by decreases within wet treatments in abundance and biomass at both Tank sites and in germination and survival at JH Tank N. Given the extreme drought in 2011, we believe the peak minimum moistures observed here were particularly important to the peak *Triadica* biomass, but we should not expect reduced reinvasion in wetter pots. However, we think increased burial of *Triadica* seeds due to movement of sediment into wet pots is the mechanism reducing success here. Thus, interspecific interactions reduced *Triadica* success but propagule availability

appears to most strongly limit *Triadica* reinvasion pressure at JH Tank sites. Native plants performed well (graminoid biomass peaked in JH Tank N) but successful restoration will require significant *Triadica* control efforts given its high reinvasion pressure, though perhaps not for long given its apparently limited seedbanks.

High clay JH sites (Fire N and S) could be said to have had the opposite set of problems; apparently sufficient propagules but high flood stress resulted in mediocre *Triadica* performance. JH Fire sites had the highest average moistures (54-55%) and average depths (~1.3 cm), and high minimum moistures (17-20%) and soil N (0.25-0.26%). Higher average depths generally reduced *Triadica* reinvasion and wet pots (whose soil surfaces 5 cm below grade subjected plants to more frequent and intense flooding) had reduced germination, abundance and, in JH Fire S, survival. While these decreases were among the largest observed, increases in germination with TSA were the smallest, TSA had no effect on abundance, and, in JH Fire N, TSA reduced survival. NSA effects were mixed, decreasing germination but increasing survival in JH Fire S. Thus, these sites with the most flooding benefited little from TSA, saw mixed interspecific effects and had strong negative effects in wetter treatments, suggesting flood stress primarily limited *Triadica* reinvasion in JH Fire sites. This may seem strange given the record 2011 drought, but flooding was common in years 1 and 2 and our moisture treatments only redirected rainfall, meaning they differed little without rain in 2011. Native plant performance was also mediocre, so successful restoration may require greater reintroduction effort but should only require moderate *Triadica* control effort.

University of Houston Coastal Center (UH) sites were highly fertile with little stress and produced the highest *Triadica* abundances with high individual performance.

UH sites had high average moistures (50-52%), intermediate to high minimum moistures (13-14% in Pipe N and S; 16-17% in Can E and W), intermediate average depths (0.2-0.3 cm), and intermediate (0.23-0.27% in Pipe N and S) to the highest soil N (0.34-0.37% in Can E and W). Moisture treatments had a few idiosyncratic effects but were generally unimportant. TSA, however, increased *Triadica* germination and abundance in all four UH sites and survival and biomass in two sites. NSA had little effect but reduced *Triadica* survival in UH Pipe N and tended to increase germination in UH Can W. Given the intermediate moisture conditions, overall high survival, strong effects of TSA, and weak effects of NSA, it seems clear that propagule availability is limiting *Triadica* reinvasion in UH sites, but not very strongly because pots without TSA showed relatively high *Triadica* success. Natives did relatively poorly here, which may be due to *Triadica* prevalence. Successful restoration will likely require considerable long-term *Triadica* control efforts given its high reinvasion pressure and robust seedbanks.

Support for the 'outgrow the stress' hypothesis

Propagule availability – As predicted by the 'outgrow the stress' hypothesis, reinvasion pressure increased with greater propagule abundance, which was demonstrated by increases in reinvasion with TSA in UH and sandy JH sites. The relative impact of propagule availability also decreased as abiotic stress increased, as exhibited by weaker effects of TSA in more stressful KP Can E and clay JH sites. We even verified that environmental extremes can "trump" propagule availability by showing that TSA had no effect in the driest KP Levee and KP War W sites. However, we saw no evidence of reinvasion pressure plateauing when propagule density reaches an upper threshold. This

may be because none of the study sites had sufficiently abundant propagules, but we previously hypothesized that spatial saturation would be common (Gabler and Siemann 2012). These results generally support the conclusions drawn by Simberloff (2009) in his review of propagule pressure, although they contradict the claim that abundant propagules could overcome limitations imposed by the physical environment (Von Holle and Simberloff 2005).

Abiotic niche – As predicted, reinvasion pressure of *Triadica* was a function of environmental factors, namely soil moisture and N content. Although predicted unimodal relationships were significant in nearly all cases, they were sometimes only marginally more predictive than, and in some cases inferior to, linear relationships. This does not preclude unimodal relationships, however, because these can appear linear if only the upper or lower range of a parameter is sampled. The frequency and intensity of stress are perhaps more important than optimality of average conditions, and long term averages are not necessarily good representations of extreme events, especially when observations are limited. This supports the seminal 'safe sites' concept holding that invasion mandates sites free of specific hazards (Harper 1977). Results are also consistent with predictions of more modern conceptions of 'safe sites' that account for spatiotemporal variation in both hazards (e.g. abiotic stress) and interspecific interactions that may mediate the impacts hazards have on invaders (e.g. Davis et al. 2000, Shea and Chesson 2002, Tilman 2004). Our observations of relatively very low *Triadica* performance in pots without TSA in the low-stress JH Tank sites is evidence that low propagule abundance can override environmental effects. We observed no direct evidence of interspecific interactions mediating abiotic effects on reinvasion.

Interspecific interactions – As predicted, competition reduced survival and performance of *Triadica*, but the effects were not observed in all sites. We did see minimal evidence of native plants facilitating *Triadica* and vice versa. Negative correlations between metrics of native success and many factors that promoted *Triadica* success strongly suggest that competition with *Triadica* is the major factor limiting reestablishment of native species. The importance of competition was influenced as expected by environmental context, but clear environmental thresholds where particular interactions became more important were not observed. That is, there were no apparent abiotic trends connecting sites where NSA or TSA affected *Triadica* or native success, respectively. As expected, competition appeared to be the most important interspecific interaction influencing reinvasion pressure, and *Triadica* was consistently the superior competitor. These findings are also consistent with modern spatiotemporal invasion hypotheses described above (e.g. Davis et al. 2000, Shea and Chesson 2002, Tilman 2004).

Broader implications for restoration and exotic species management

This work further demonstrates the importance of variation in reinvasion pressure to restoration outcomes and costs. Our findings also demonstrate the potential merit of using models based on fluctuating plant niches and habitat environmental patterns to make both short-and longer-term predictions of reinvasion pressure. Such forecasts can enhance predictions of outcomes and costs of restoration and exotic management, which are crucial to ecological and economic planning. More directly, forecasts of reinvasion

pressure can improve restoration and exotic management efficiency at local and landscape scales by informing optimal management strategies and/or site selection.

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Table 5.1. Results of ANODEV chi-square tests (a form of likelihood ratio test) for total *Triadica* germination, final *Triadica* abundance and native plant species richness (count data), and for *Triadica* survival (proportion data), as well as results of ANCOVA F-tests for aboveground *Triadica* biomass and native species Shannon diversity. Legend: NSA – native seed addition, TSA – *Triadica* seed addition.

	total *Triadica* germination			final *Triadica* abundance			*Triadica* survival (final abund. / cum. germ)			final *Triadica* aboveground biomass			native species richness			native species diversity (H')		
factor	d.f.	X^2	*p*	d.f.	X^2	*p*	d.f.	F_{339}	*p*	d.f.	F_{522}	*p*	d.f.	X^2	*p*	d.f.	F_{522}	*p*
average moisture	1	109.09	**<0.0001**	1	50.07	**<0.0001**	1	5.40	**0.0202**	1	0.39	0.53	1	237.10	**<0.0001**	1	136.85	**<0.0001**
min moisture	1	7.36	**0.0067**	1	18.17	**<0.0001**	1	61.22	**<0.0001**	1	86.13	**<0.0001**	1	22.93	**<0.0001**	1	7.75	**0.0056**
average water depth	1	47.37	**<0.0001**	1	37.78	**<0.0001**	1	8.31	**0.0039**	1	7.62	**0.0060**	1	0.16	0.69	1	0.04	0.84
soil N content	1	62.72	**<0.0001**	1	16.55	**<0.0001**	1	0.56	0.46	1	37.97	**<0.0001**	1	35.17	**<0.0001**	1	25.78	**<0.0001**
venue	2	8.99	**0.0111**	2	32.75	**<0.0001**	2	45.83	**<0.0001**	2	1.64	0.20	2	11.81	**0.0027**	2	4.71	**0.0095**
site(venue)	7	136.71	**<0.0001**	7	35.77	**<0.0001**	7	31.79	**<0.0001**	7	1.50	0.17	7	110.78	**<0.0001**	7	12.04	**<0.0001**
moisture(site,venue)	22	64.95	**<0.0001**	22	40.76	**0.0088**	22	37.06	**0.0233**	22	1.97	**0.0059**	22	65.21	**<0.0001**	22	2.38	**0.0005**
NSA(site,venue)	11	21.83	**0.0257**	11	18.09	0.08	11	23.80	**0.0136**	11	0.60	0.83	11	32.49	**0.0006**	11	2.20	**0.0137**
TSA(site,venue)	11	442.07	**<0.0001**	11	140.48	**<0.0001**	10	36.61	**0.0001**	11	8.45	**<0.0001**	11	14.06	0.23	11	1.10	0.36
moist*NSA(site,venue)	22	52.39	**0.0003**	22	25.49	0.27	22	29.31	0.14	22	0.91	0.58	22	33.12	0.06	22	1.70	**0.0259**
moist*TSA(site,venue)	22	25.87	0.26	22	35.04	**0.0383**	19	27.80	0.09	22	0.67	0.87	22	24.48	0.32	22	1.37	0.12
NSA*TSA(site,venue)	11	8.32	0.68	11	5.22	0.92	9	4.20	0.90	11	1.89	**0.0389**	11	14.64	0.20	11	0.84	0.60
moist*NSA*TSA(site,venue)	22	47.38	**0.0013**	22	12.46	0.95	14	0.00	1.00	22	0.63	0.90	22	34.07	**0.0483**	22	1.32	0.16

Table 5.2. Results of ANCOVA F-tests for aboveground biomass of native plants in total and by functional group. Legend: NSA – native seed addition, TSA – *Triadica* seed addition.

	total native biomass			native graminoid biomass			native forb biomass			native woody biomass			native vine biomass			other native biomass		
factor	d.f.	F	*p*	d.f.	F	*p*	d.f.	F	*p*	d.f.	F	*p*	d.f.	F	*p*	d.f.	F	*p*
average moisture	1	0.82	0.37	2	1.31	0.25	2	20.42	**<0.0001**	2	2.42	0.12	2	1.18	0.28	2	1.77	0.18
min moisture	1	0.14	0.71	1	3.70	0.06	1	8.42	**0.0039**	1	0.02	0.90	1	0.03	0.86	1	0.45	0.50
average water depth	1	0.96	0.33	1	0.02	0.90	1	0.56	0.46	1	1.02	0.31	1	2.94	0.09	1	0.01	0.92
soil N content	1	4.14	**0.0425**	1	0.45	0.50	1	2.29	0.13	1	6.16	**0.0135**	1	2.20	0.14	1	0.02	0.89
venue	2	4.34	**0.0137**	1	4.41	**0.0128**	1	0.42	0.65	1	3.24	**0.0401**	1	0.46	0.63	1	0.19	0.83
site(venue)	7	2.22	**0.0322**	7	1.47	0.18	7	11.98	**<0.0001**	7	2.76	**0.0083**	7	1.09	0.37	7	1.33	0.23
moisture(site,venue)	22	0.81	0.72	22	0.65	0.89	22	2.79	**<0.0001**	22	0.81	0.72	22	0.91	0.58	22	1.05	0.41
NSA(site,venue)	11	0.74	0.70	11	2.27	**0.0108**	11	3.19	**0.0004**	11	0.54	0.88	11	0.65	0.79	11	0.96	0.48
TSA(site,venue)	11	0.83	0.61	11	2.38	**0.0074**	11	2.90	**0.0011**	11	0.75	0.69	11	0.79	0.65	11	1.13	0.33
moist*NSA(site,venue)	22	0.40	0.99	22	0.74	0.79	22	2.19	**0.0017**	22	0.33	1.00	22	1.09	0.36	22	0.96	0.52
moist*TSA(site,venue)	22	0.54	0.96	22	0.60	0.92	22	2.13	**0.0023**	22	0.51	0.97	22	1.12	0.32	22	1.05	0.40
NSA*TSA(site,venue)	11	2.52	**0.0044**	11	2.89	**0.0011**	11	0.82	0.62	11	2.56	**0.0038**	11	1.22	0.27	11	1.03	0.42
moist*NSA*TSA(site,venue)	22	0.82	0.71	22	0.87	0.63	22	5.05	**<0.0001**	22	0.83	0.69	22	0.81	0.71	22	1.06	0.39

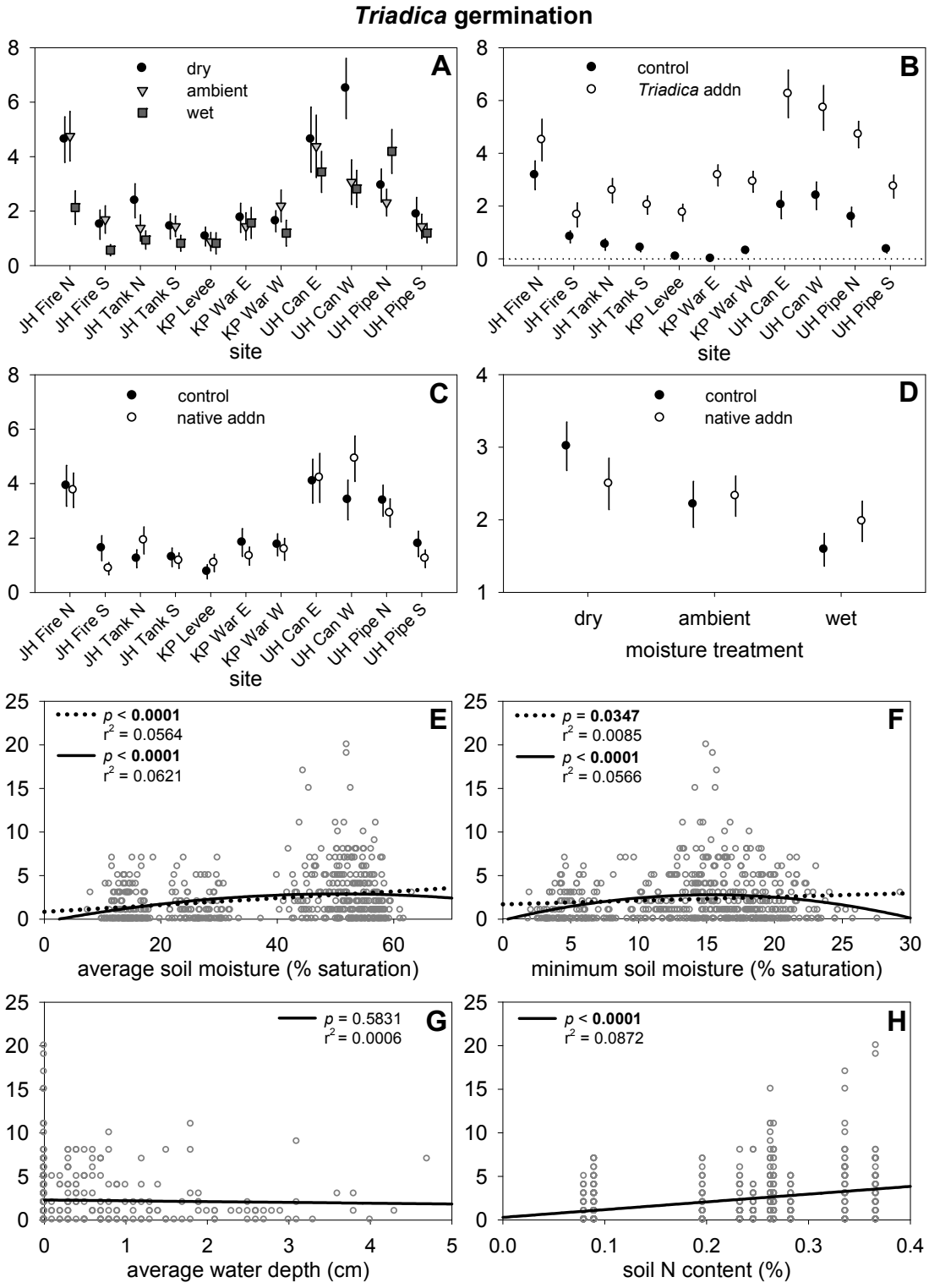

Figure 5.1. Cumulative *Triadica* germination per pot observed over three years (means ± SE) broken down by site and moisture treatments (A), site and *Triadica* seed addition

treatments (B), site and native seed addition treatments (C), and moisture and native seed addition treatments (D), as well as correlations between *Triadica* germination and average soil moisture (E), minimum soil moisture (F), average water depth (G) and soil N content (H).

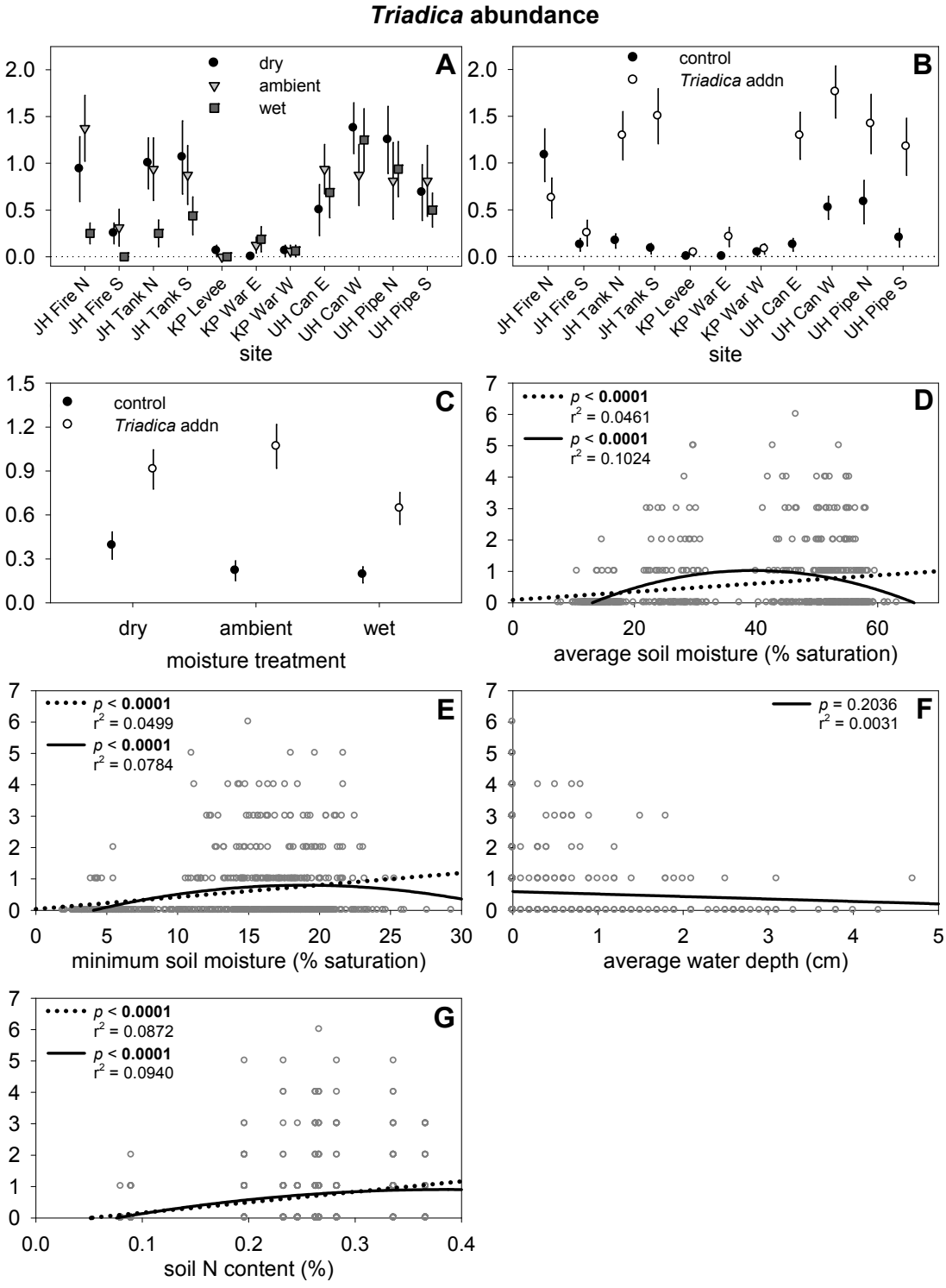

Figure 5.2. Final *Triadica* abundance per pot in fall of year 3 (means ± SE) broken down by site and moisture treatments (A), site and *Triadica* seed addition treatments (B), and

moisture and *Triadica* seed addition treatments (C), as well as correlations between *Triadica* abundance and average soil moisture (D), minimum soil moisture (E), average water depth (F) and soil N content (G).

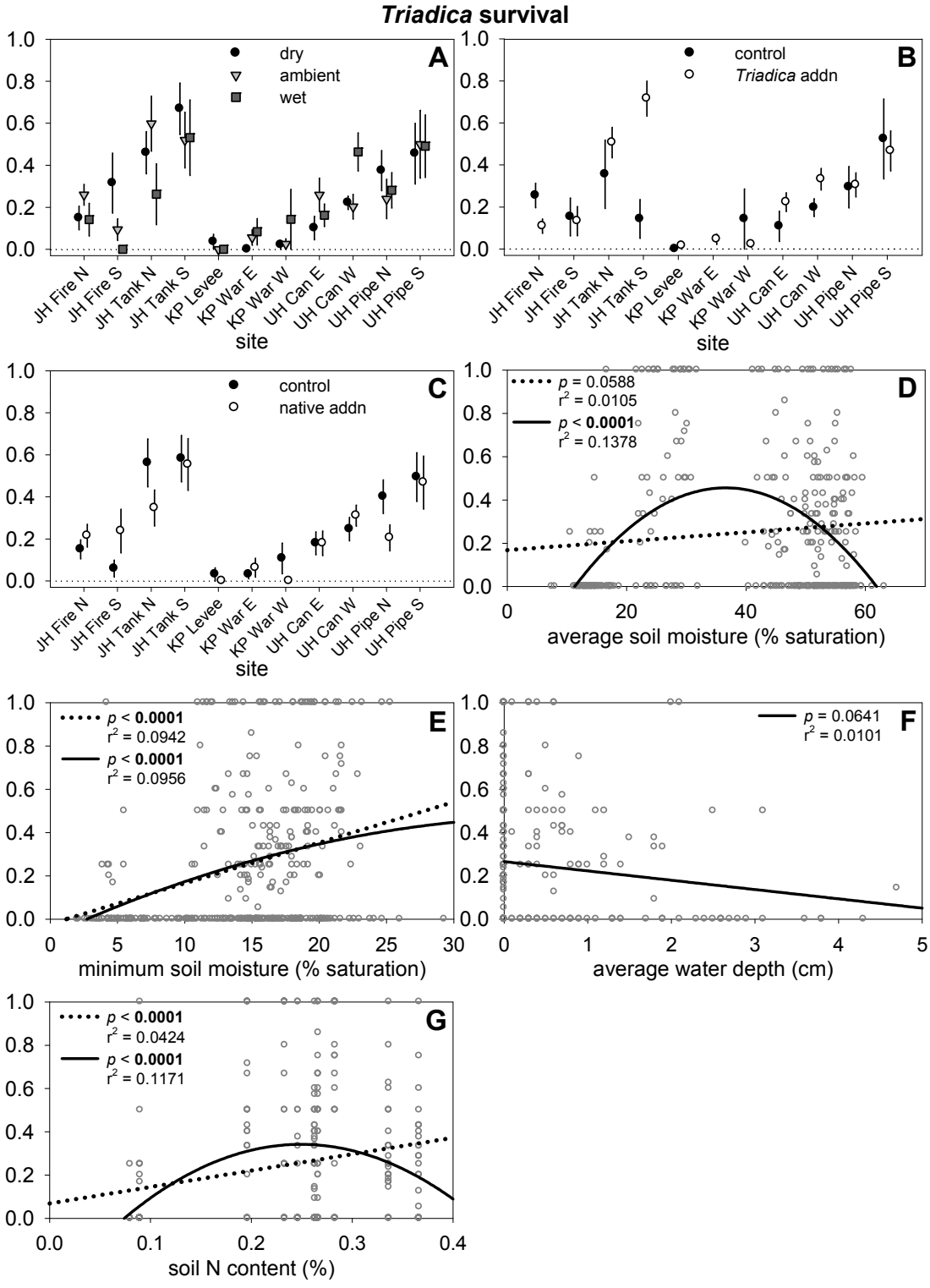

Figure 5.3. Overall *Triadica* survival (final abundance / cumulative germination) (means ± SE) broken down by site and moisture treatments (A), site and *Triadica* seed addition

treatments (B), and site and native seed addition treatments (C), as well as correlations between *Triadica* survival and average soil moisture (D), minimum soil moisture (E), average water depth (F) and soil N content (G).

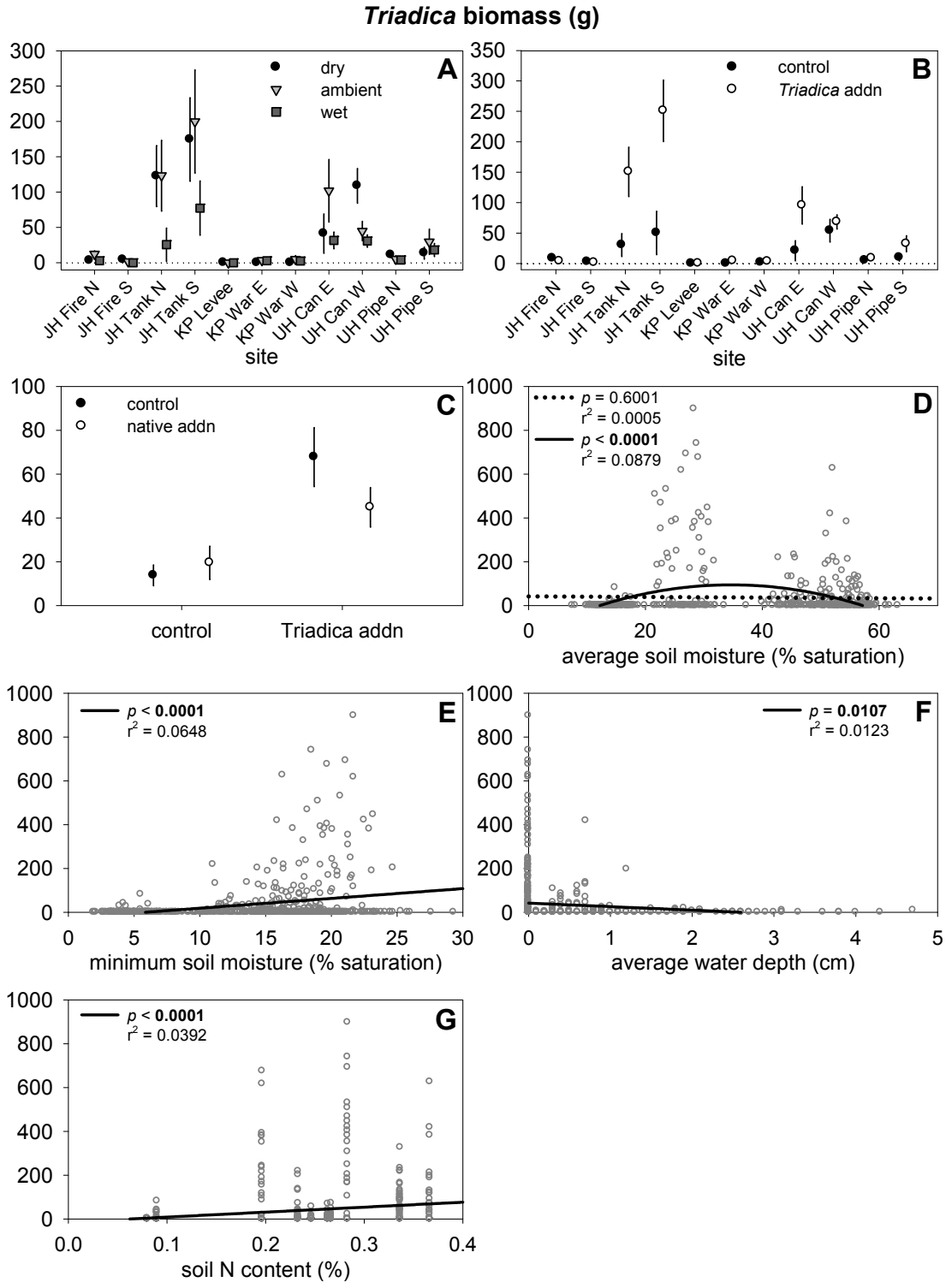

Figure 5.4. Dry *Triadica* biomass per pot after three growing seasons (means ± SE) broken down by site and moisture treatments (A), site and *Triadica* seed addition

treatments (B), and *Triadica* and native seed addition treatments (C), as well as correlations between *Triadica* biomass and average soil moisture (D), minimum soil moisture (E), average water depth (F) and soil N content (G).

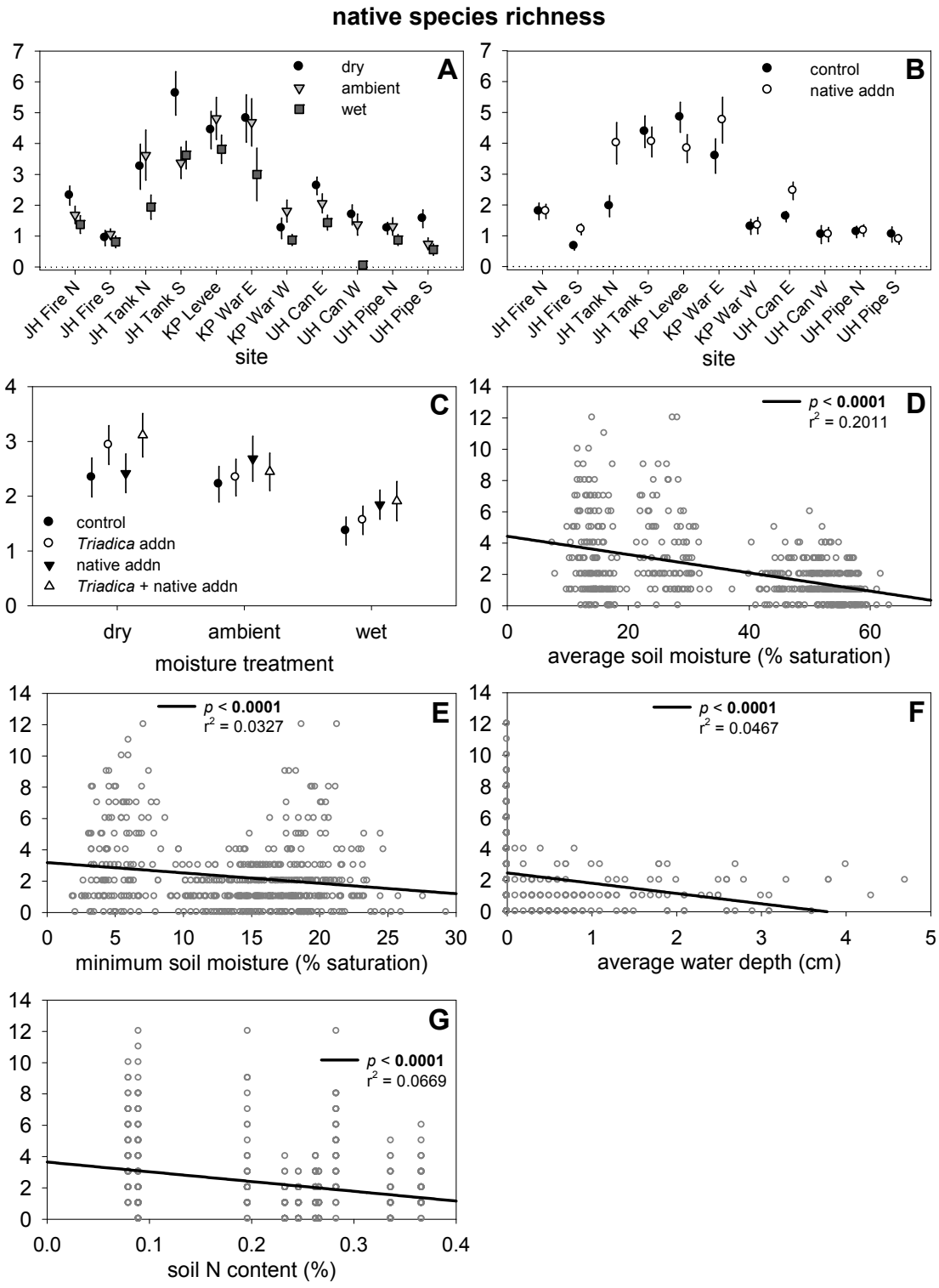

Figure 5.5. Native plant species richness per pot after three growing seasons (means ± SE) broken down by site and moisture treatments (A), site and native seed addition

treatments (B), and moisture and *Triadica* and native seed addition treatments (C), as well as correlations between native species richness and average soil moisture (D), minimum soil moisture (E), average water depth (F) and soil N content (G).

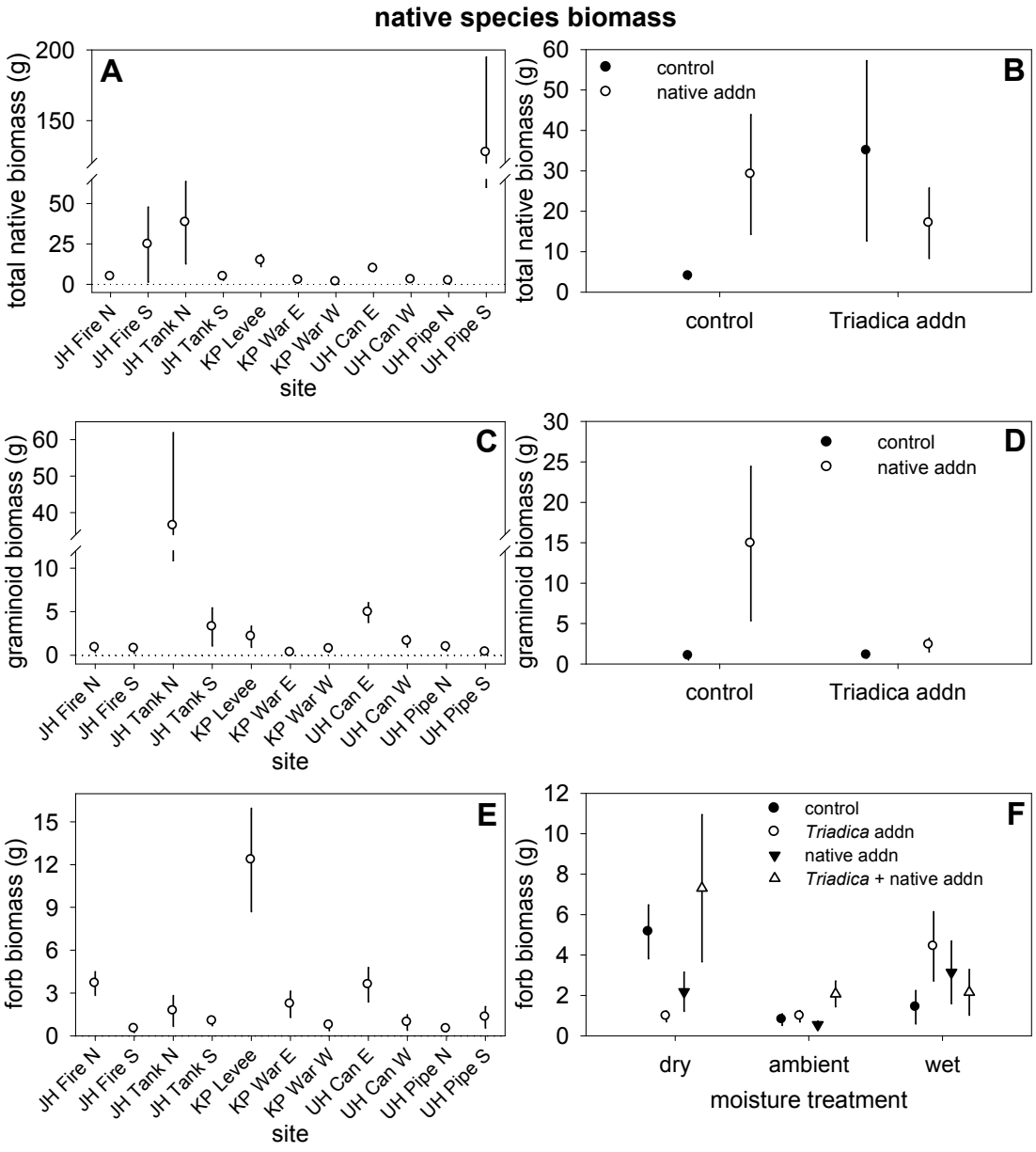

Figure 5.6. Native plant dry biomass after three growing seasons (means ± SE). Total native biomass is broken down by site (A) and *Triadica* and native seed addition treatments (B). Graminoid biomass is shown for individual sites (C) and *Triadica* and native seed addition treatments (D). Forb biomass is broken down by site (E) and by moisture and *Triadica* and native seed addition treatments (F).

SUPPORTING INFORMATION

Appendix 5.S1. List of plant species included in our native seed mix

Table 5.S1. Coordinates of our eleven experimental restoration sites

Table 5.S2. ANOVA results testing effects of manipulations on soil moisture metrics

Table 5.S3. Equations of best fit regression lines shown in Figs. 1-5

Figure 5.S1. Graphical summary of plant community composition at each restoration site

Appendix 5.S1. List of native plant species included in our native seed mix. All native seed was obtained commercially from Native American Seed (Junction, Texas, USA).

Agalinis heterophylla (Nutt.) Small ex Britt.	prairie agalinis
Agave americana L.	American aloe
Ambrosia spp.	ragweed
Andropogon gerardii Vitman	big bluestem
Andropogon glomeratus (Walter) Britton, Sterns & Poggenb.	bushy bluestem
Andropogon ternarius Michx.	splitbeard bluestem
Andropogon virginicus L.	broomsedge bluestem
Aristida spp.	three-awn
Asteraceae	aster
Bouteloua curtipendula (Michx.) Torr.	sideoats grama
Carex spp.	true sedge
Chamaecrista fasciculata (Michx.) Greene	partridge pea
Coreopsis lanceolata L.	lanceleaf coreopsis
Coreopsis tinctoria Nutt.	plains coreopsis
Croton spp.	croton
Cyperus spp.	flatsedge
Desmanthus illinoensis (Michx.) MacMill. ex B.L. Rob. & Fernald	Illinois bundleflower
Diodia teres Walter	rough buttonweed
Dracopis amplexicaulis (Vahl) Cass.	clasping coneflower
Dysphania ambrosioides (L.) Mosyakin & Clemants	epazote
Elionurus tripsacoides Humb. & Bonpl. ex Willd.	balsamscale
Elymus canadensis L.	prairie wildrye
Elymus virginicus L.	Virginia wildrye
Eragrostis secundiflora J. Presl	red lovegrass
Erigeron compositus Pursh	cutleaf daisy
*Eryngium yuccifolium*Michx.	rattlesnake master
Gaillardia pulchella Foug.	indian blanket
Grindelia spp.	gumweed
Helianthus spp.	sunflower
Helianthus maximiliani Schrad.	Maximilian sunflower

Iva annua L.	sumpweed
Iva angustifolia Nutt. ex DC.	narrowleaf marsh elder
Leptochloa dubia (Kunth) Nees	green sprangletop
Liatris pycnostachya Michx.	prairie blazing star
Lupinus texensis Hook.	Texas bluebonnet
Monarda citriodora Cerv. ex Lag.	lemon beebalm
Muhlenbergia capillaris (Lam.) Trin.	hairawn muhly grass
Oenothera speciosa Nutt.	pink evening primrose
Panicum virgatum L.	switchgrass
Paspalum spp.	paspalum
Paspalum floridanum Michx.	Florida paspalum
Polygonum spp.	smartweed
Ratibida columnifera (Nutt.) Woot. & Standl.	prairie coneflower
Ratibida peduncularis (Torr. & A. Gray) Barnhart	Mexican hat
Rhynchospora spp.	horned beaksedge
Rudbeckia maxima Nutt.	giant coneflower
Rudbeckia hirta L.	black-eyed Susan
Salvia spp.	sage
Salvia azurea Michx. ex Lam. var. *grandiflora* Benth.	pitcher sage
Schizachyrium scoparium (Michx.) Nash	little bluestem
Secale cereale L.	cereal rye
Setaria parviflora (Poir.) Kerguélen	knotroot bristlegrass
Solidago canadensis var. scabra	tall goldenrod
Sorghastrum nutans (L.) Nash	indiangrass
Sporobolus compositus (Poir.) Merr	tall dropseed
Sporobolus cryptandrus (Torr.) A. Gray	sand dropseed
Tridens albescens (Vasey) Woot. & Standl.	white tridens
Tridens flavus (L.) Hitchc.	purpletop tridens
Tridens muticus (Torr.) Nash	slim tridens
Tridens strictus (Nutt.) Nash	longspike tridens
Tripsacum dactyloides (L.) L.	eastern gamagrass
Verbena spp.	vervain

Table 5.S1. Locations of our eleven experimental restoration sites in degree-minute-second (DMS) format.

short name	descriptive name	latitude	longitude
JH Fire N	Justin Hurst WMA - Fire Break North	28°57'39.20"N	95°28'38.34"W
JH Fire S	Justin Hurst WMA - Fire Break South	28°57'36.58"N	95°28'37.55"W
JH Tank N	Justin Hurst WMA - Cattle Tank North	28°56'20.06"N	95°26'15.86"W
JH Tank S	Justin Hurst WMA - Cattle Tank South	28°56'16.18"N	95°26'10.36"W
KP Levee	Katy Prairie - Levee	29°56'9.56"N	95°51'7.37"W
KP War E	Katy Prairie - Warren Ranch East	29°56'15.97"N	95°53'29.26"W
KP War W	Katy Prairie - Warren Ranch West	29°56'14.71"N	95°53'33.07"W
UH Can E	UH Coastal Center - Canal East	29°22'40.07"N	95°2'27.51"W
UH Can W	UH Coastal Center - Canal West	29°22'40.50"N	95°2'30.78"W
UH Pipe N	UH Coastal Center - Pipeline North	29°22'45.66"N	95°1'54.09"W
UH Pipe S	UH Coastal Center - Pipeline South	29°22'43.94"N	95°1'52.54"W

Table 5.S2. ANOVA results examining the effects of venue, site, moisture treatments, native seed addition (NSA), *Triadica* seed addition (TSA) and their interactions on three key metrics of soil moisture.

	average soil moisture			average water depth			minimum soil moisture		
factor	d.f.	F_{522}	*p*	d.f.	F_{522}	*p*	d.f.	F_{522}	*p*
venue	2	9541.10	**<0.0001**	2	164.56	**<0.0001**	2	1243.51	**<0.0001**
site(venue)	8	767.62	**<0.0001**	8	92.81	**<0.0001**	8	21.47	**<0.0001**
moisture(site,venue)	22	25.11	**<0.0001**	22	52.68	**<0.0001**	22	3.21	**<0.0001**
NSA(site,venue)	11	1.60	0.10	11	0.40	0.95	11	1.33	0.21
TSA(site,venue)	11	0.59	0.84	11	1.03	0.42	11	0.83	0.61
moist*NSA(site,venue)	22	1.37	0.12	22	0.34	1.00	22	0.55	0.95
moist*TSA(site,venue)	22	2.13	**0.0024**	22	0.74	0.79	22	1.02	0.44
NSA*TSA(site,venue)	11	0.48	0.91	11	0.56	0.86	11	0.32	0.98
moist*NSA*TSA(site,venue)	22	0.82	0.70	22	0.54	0.96	22	0.64	0.89

Table 5.S3. Equations of best fit simple regression lines show in Figures 5.1-5.5.

figure	linear	quadratic
1E	$y = 0.0389x + 0.8322$	$y = -0.0012x^2 + 0.1264x - 0.3188$
1F	$y = 1.6859x + 0.0426$	$y = -0.0124x^2 + 0.3803x - 0.1437$
1G	$y = -0.0910x + 2.2989$	
1H	$y = 8.8896x + 0.2863$	
2D	$y = 0.0131x + 0.0871$	$y = -0.0015x^2 + 0.1159x -1.2644$
2E	$y = 0.0383x + 0.0378$	$y = -0.0036x^2 + 0.1368x - 0.4957$
2F	$y = -0.0783x + 0.5977$	
2G	$y = 3.3399x - 0.1729$	$y = -9.4027x^2 + 7.2614x - 0.4961$
3D	$y = 0.0021x + 0.1677$	$y = -0.0007x^2 + 0.0522x - 0.4987$
3E	$y = 0.0188x - 0.0225$	$y = -0.0004x^2 + 0.0284x - 0.0745$
3F	$y = -0.0430x - 0.2655$	
3G	$y = 0.7588x + 0.0686$	$y = -11.1244x^2 + 5.5468x - 0.3496$
4D	$y = -0.1432x + 41.8623$	$y = -0.1870x^2 + 12.9755x - 130.5324$
4E	$y = 4.4701x - 26.1984$	
4F	$y = -16.0679x + 41.7701$	
4G	$y = 226.9498x - 14.1356$	
5D	$y = -0.0584x - 4.4395$	
5E	$y = -0.0664x - 3.1891$	
5F	$y = -0.6563x + 2.4793$	
5G	$y = -6.2241x + 3.6514$	

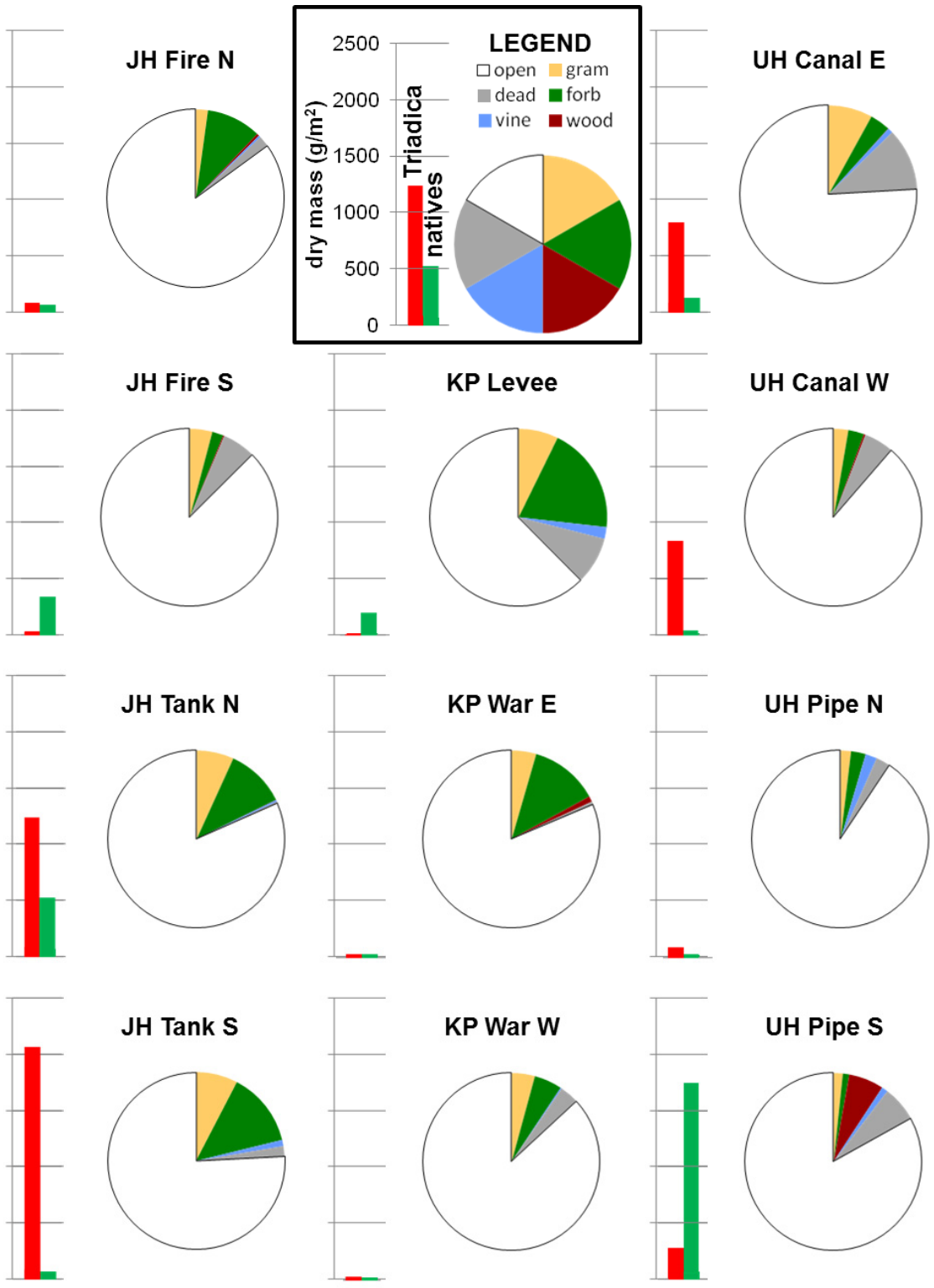

Figure 5.S1. Graphical summary of plant community compositions within mesocosm pots at each of our eleven experimental restoration sites. Each pair of bar and pie charts

correspond to one site. Bar graphs denote dry biomass in g/m^2, with gray reference lines every 500 g/m^2. Pie charts denote total percent cover represented by particular functional groups of native plants only; the "dead" group includes standing but dead plants (i.e. not litter) of any functional group. *Legend*: Red bars – mean total *Triadica* biomass; green bars – mean total native plant biomass; gold wedges – graminoids; green wedges – forbs; brown wedges – woody species; blue wedges – vines or climbers; gray wedges – dead plants; white wedges – open ground (including litter).